

EFFECTS OF LOCAL PLANT NEIGHBORHOOD ON PLANT HERBIVORY IN  
PERENNIAL POLYCULTURE CROPPING SYSTEMS

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Perennializing grain cropping systems has been proposed as a way to mitigate the challenges facing agriculture in the future due to crop intensification. Crop intensification is characterized by utilizing more land and inputs, less crop diversity, and greater crop density. Perennial cropping systems use native prairie as a model and model diverse prairie communities with perenniality and polyculture. Perennial cropping systems allow for complex planting arrangements (e.g. crop frequency, intercrops, and row spacings) that could confer specialist insect pest resistance via reduced host plant apparency, changes in herbivore attraction, and host plant tissue quality. The three chapters in this dissertation examine these themes of perennial polyculture and effects of spatial heterogeneity on insect abundance.

The first chapter compares insect herbivore, predator and parasitoid, pollinator, and detritivore abundance, morphospecies richness, and biovolume among hayed grasslands, and wheat fields. Pollinators and detritivores were more abundant, had greater biovolume, and were more species-rich in hayed grasslands than in wheat fields. Therefore, insects may provide more pollination and decomposition ecosystem services in hayed grasslands. However, grasslands and wheat fields supported comparable numbers of herbivores, suggesting that herbivore densities in grasslands are not any more limited by predators and parasitoids than herbivore densities in wheat fields.

The second chapter examined insect herbivore foliar feeding on a legume, *Desmanthus illinoensis*, which is in the early stages of development as a perennial grain crop. Insect herbivory was examined in the context of prairies. Local neighborhood grass cover strongly

influenced insect herbivore foliar feeding; greater grass cover within the plant neighborhood resulted in lesser foliar herbivory. Our results suggest that incorporation of crop diversity, through the addition of a grass, in perennial agroecosystems with *D. illinoensis* could result in reduced foliar feeding by a specialist herbivore.

The third chapter examined a legume (*D. illinoensis*)-grass (*Thinopyrum intermedium*) intercrop with row spacing and initial frequency of legume seed treatments. The bicultures were productive which suggests that incorporating crop diversity could benefit perennial polyculture. However, row spacing and seeding frequency had little effect on plant herbivory in this agroecosystem, most likely due to dominance of generalist herbivores.

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CURRICULUM VITAE

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**Title:** COMPARISON OF INSECT DIVERSITY BETWEEN ANNUAL MONOCULTURE AND  
PERENNIAL POLYCULTURE CROP FIELDS

**Abstract**

During the twentieth century, agricultural systems became increasingly intensified through the use of more land and inputs, less crop diversity, and greater crop density. Wheat fields are an example of an intensified agricultural system. In contrast, hayed grasslands are able to sustain comparable annual above-ground biomass harvests to that of annual wheat fields but without the intensification of wheat fields. With increased crop intensification in agroecosystems it is expected there will be greater insect abundance, less predator control, and decreased insect species richness. The resource concentration hypothesis predicts that denser plant stands (e.g. wheat monocultures) will attract greater densities of specialist insect herbivores due to higher feeding rates and easier location of host plants. The enemies hypothesis predicts that there will be greater numbers of insect predators and parasitoids in the hayed grasslands due to the greater plant host diversity in the hayed grasslands. Host plant compositional differences between hayed grasslands and wheat fields may also affect pollinators in that hayed grasslands are more likely to have flowering plants and therefore are expected to have more pollinators. Five sites with hayed grassland and adjacent annual wheat field pairs were sampled using a sweep net. The insect samples from sweep netting were processed to family for insect abundance, morphospecies, and biovolume. Our results did not support our predictions of lesser herbivore abundance and greater predator and parasitoid abundance in hayed grassland. However, our results did support our prediction of greater numbers of pollinators in hayed grassland. There was not a statistically significant difference in average insect abundance or biovolume among the hayed grasslands and wheat fields. However, morphospecies richness was greater in hayed

grasslands than in wheat fields. Pollinators and detritivores were more abundant, had greater biovolume, and were more species-rich in hayed grasslands than in wheat fields. Therefore, in contrast to annual wheat fields, insects may provide more pollination and decomposition ecosystem services in hayed grasslands. However, grasslands and wheat fields support comparable numbers of herbivores and our results suggest that herbivore densities in grasslands are not any more limited by predators and parasitoids than herbivore densities in wheat fields. Further investigation into insect diet breadth and more intensive insect sampling of hayed grasslands and wheat fields could further our knowledge about the potential ecosystem service of insect herbivore control in these agroecosystems.



## **Introduction**

During the twentieth century, agricultural systems became increasingly intensified through the use of more land and inputs, less crop diversity, and greater crop density (Pimentel et al. 1976; Jackson 1980). With intensification, agricultural systems had significant increases in yields. However, in more recent years the rate of increase has slowed and there are ongoing concerns about the sustainability of intensified agricultural systems (Pimentel et al. 1976; Jackson 1980; Matson 1997; Glover 2010).

As an intensified agricultural crop, annual wheat fields are actively managed to maximize seed yield through fertilizer inputs, tillage, monoculture, and variety selection (Glover et al. 2010). In contrast, hayed grasslands, with their sustained annual above-ground biomass harvest and ability to maintain ecosystem services, offer an excellent example of a sustainable agricultural system (Glover et al. 2010). Wheat fields and hayed grasslands represent two very different plant communities and thus could have different interactions with insects due to differences in productivity, plant density, diversity, and composition. Wheat fields are a monoculture (low diversity and high density) of a domesticated grass while hayed grasslands are diverse native grassland plant communities (low density) with multiple plant species and functional groups (e.g. forbs, grasses, legumes). Wheat fields differ from hayed grasslands in that they have lesser plant species richness, a greater reliance on disturbance, and a greater reliance on exogenous sources of nitrogen (Crews 2005). Wheat fields and hayed grasslands also differ in the types of crops they produce; hayed grasslands produce livestock fodder while wheat fields produce grain for humans and livestock. However, they are similar in that they both have an annual harvest and removal of above-ground biomass (Glover 2010).

Insect herbivores are often responsible for crop yield loss through herbivory (Andow 1991). Insects can also provide important ecosystem services such as biological control (Crowder and Jabbour 2014), pollination (Klein et al. 2007), and promote nutrient cycling and soil fertility (Weisser and Siemann 2004). Dense monocultures, such as wheat fields, have been hypothesized to facilitate larger populations of herbivores (Root 1973; Andow 1991). The resource concentration hypothesis predicts that denser plant stands (e.g. wheat monocultures) will attract greater densities of specialist insect herbivores due to higher feeding rates and easier location of host plants (Root 1973). A review that supports this hypothesis examined 209 studies on 287 arthropod species in mono- and polyculture and found insect population densities were less in polyculture for 51.9% of insect species and greater in polyculture for 15.3% of insect species (Andow 1991). Biocontrol by natural enemies, such as predators and parasitoids, can also be weakened by reducing crop diversity (Tylianakis et al. 2007; Macfadyen et al. 2009). The enemies hypothesis predicts that insect predator densities will be greater and predators will be more efficient in killing herbivores in cropping systems that are more species rich (e.g. hayed grasslands; Root 1973). Insect predator densities are predicted to be greater in plant species rich cropping systems due to conditions in species rich cropping systems that decrease predator emigration or local extinction such as: greater abundance of suitable predator microhabitats (e.g. increased ground cover), greater herbivore richness (e.g. alternate prey are available when other prey are scarce), and supply of pollen and nectar resources (Root 1973; Letourneau 1987). Here, predaceous insects are posited to be generalists (but see Stiling et al. 2003) or to benefit from the greater richness in insect prey available within diverse host plant stands (Root 1973).

The green world hypothesis predicts that detritivores, plants, and predators and parasitoids are resource limited while herbivores are consumer limited (Hairston et al., 1960). Our hayed

grasslands had greater and more species rich above-ground biomass than the wheat fields which led us to predict that detritivores and predators and parasitoids would be more abundant in the hayed grassland than in the wheat fields. The resource concentration hypothesis predicts that specialist herbivores would be less abundant in the hayed grassland because host plants would be less abundant than in the wheat fields (Root 1973). However, species richness of host plants was greater in the hayed grasslands (Glover et al. 2010) and we predicted there would be greater morphospecies richness of herbivores and detritivores. Compositional effects of hayed grasslands were likely to be especially important for pollinators since hayed grasslands had flowering plants while wheat fields did not; we expected to find more pollinators and more pollinator morphospecies in hayed grassland.

## **Methods**

Four sites with hayed grassland and adjacent annual wheat fields were sampled from 17-27 June 2007 using a sweep net. The sites were: New Cambria (hayed grassland: 38.53N, 97.32W; wheat: 38.53N, 97.32W; Saline County, Kansas), Niles (hayed grassland: 38.58N, 97.28W; wheat: 38.53N, 97.28W; Saline County, Kansas), Goessel (hayed grassland: 38.15N, 97.22W; wheat: 38.15N, 97.22W; McPherson County, Kansas), and Five Creeks (hayed grassland: 39.22N, 97.18W; wheat: 39.22N, 97.18W; Clay County, Kansas). At a fifth site, Buckeye, the field adjacent to the hayed grassland was in soybean instead of wheat (hayed grassland: 39.02N, 97.07W; soybean: 39.02N, 97.07W; Dickinson County, Kansas). Sites were at least 8 km apart. At all sites, annual wheat fields and hayed grasslands were next to each other and sampling in each cover type occurred 37 m apart. The hayed grassland and wheat fields were sampled on the same day at each site. Sampling occurred between 10AM and 4PM at temperatures of 29-32°C and low wind velocities (<24 km/h at all sites except for New Cambria where winds were 32

km/h). At all sites, except for Buckeye where soybeans were planted, the wheat fields were in conventional wheat production using common practices for the region (e.g. crop rotation, no application of insecticide, and/or no tillage practices; Glover et al., 2010). Plant community composition and cover for all of the hayed grasslands was mostly that of native grass species (69% grass cover on average; Glover et al., 2010). Plant species richness among all functional groups in the hayed grasslands was, on average, 29 species (Glover et al., 2010). Plant species in the hayed grassland were observed using ten, 1m<sup>2</sup> quadrats at each site in June 2007 (Glover et al. 2010).

Sweep sampling in the hayed grasslands and adjacent wheat fields was conducted using a sweep net along transects spaced 2 m apart within a 22 m x 22 m area. Transects were 22 m long and there were 11 transects for each hayed grassland and wheat field (22 total transects for each site). After sampling, the insects were stored in resealable plastic bags in a freezer (< 0°C). Insects were later sorted to family and morphospecies using a dissecting microscope. Functional group category for morphospecies (predator and parasite, herbivore, detritivore, or pollinator) was based upon adult feeding habits of insect family using literature review (Triplehorn and Johnson, 2004; Salsbury and White, 2000). Insect biovolume, a measure of biomass, was calculated using the volume equation of a cylinder. The average length and thickness for three insects of the same morphospecies was used for biovolume calculations. If fewer than three were available, then all available insects were measured. Insect length and thickness were measured using digital calipers.

Analysis of variance was performed (ANOVA; SPSS v.16) to examine effects of site (random), production system (fixed) on insect abundance, richness, and biovolume. Separate analyses on abundance, richness, and biovolume for each functional group were performed using the same

model. All data were transformed ( $\sqrt{y+1}$ ) to conform to normality assumptions. Type IV sum of squares was used due to an unbalanced experimental design (i.e. no wheat field at Buckeye).

Insect diversity was calculated using the loglinear  $\alpha$  diversity index due to its robustness and low sensitivity to sample size (Magurran, 1988). The Jaccard index was used to examine similarity in sweep net samples among hayed grasslands and wheat fields within each site. Loglinear  $\alpha$  and Jaccard index values were calculated using Estimates 9.1.0 (Colwell 2013).

## **Results**

There was not a statistically significant difference in average insect abundance or biovolume among the hayed grasslands and wheat fields (Tables 1 and 2; Figures 1 and 2). Overall, significantly greater numbers of morphospecies were collected in hayed grassland than in wheat (Table 3; Figure 3). Hayed grasslands had greater insect diversity than wheat fields (mean loglinear alpha hayed grassland: 27.42 S.E.: 4.0, wheat: 10.68 S.E.: 2.5).

There was very little overlap between the morphospecies collected in hayed grassland and wheat (mean Jaccard: 0.16, S.E.: 0.04); overlap between morphospecies collected in hayed grassland and wheat was least at New Cambria (Jaccard: 0.08) and Goessel (Jaccard: 0.13) and greatest at Niles (Jaccard: 0.18) and Five Creeks (Jaccard: 0.26).

## ***Herbivores***

On average, there was greater herbivore abundance and biovolume in hayed grassland than in wheat, but this difference was not statistically significant for either measure (Tables 1 and 2; Figures 1 and 2). There was significantly greater herbivore species richness in hayed grassland than in wheat (Table 3; Figure 3). Herbivore abundance was greater in hayed grassland than in wheat for all sites except for Five Creeks (Five Creeks- hayed grassland: 221 herbivores, wheat:

315 herbivores; Goessel- hayed grassland: 590 herbivores, wheat 227 herbivores; New Cambria- hayed grassland: 221 herbivores, wheat: 23 herbivores; Niles- hayed grassland: 477 herbivores, wheat: 223 herbivores). Herbivore biovolume was greater in hayed grassland for all sites except for New Cambria (Five Creeks- hayed grassland: 11,405.8 mm<sup>3</sup>, wheat: 4,216.1 mm<sup>3</sup>; Goessel- hayed grassland: 5,109.0 mm<sup>3</sup>, wheat 698.2 mm<sup>3</sup>; New Cambria- hayed grassland: 5,402.3 mm<sup>3</sup>, wheat: 14,145.7 mm<sup>3</sup>; Niles- hayed grassland: 9,315.0 mm<sup>3</sup>, wheat: 1,200.4 mm<sup>3</sup>).

Overall, most of the herbivores in the hayed grassland were Coleopterans followed by Homopterans, Dipterans, Hemipterans, Hymenopterans, Lepidopterans, and Orthopterans (Figure 4). Most of the herbivores in wheat fields were Homopterans followed by Coleopterans, Hemipterans, Dipterans, Hymenopterans, Lepidopterans, and finally Orthopterans (Figure 4). Herbivore morphospecies richness was significantly greater in hayed grassland than in wheat (mean among grasslands: 47.20 S.E.: 4.62, wheat: 20.59 S.E.:5.39). Most of the herbivorous morphospecies collected in hayed grassland were Coleopterans (Figure 4) and in wheat were Homopterans (Figure 4). Among the herbivorous beetles, most of the morphospecies were Apionids, Curculionids, and Chrysomelids. Among the Homopterans most of the morphospecies were Cicadellids.

### ***Predators and parasitoids***

While there were trends for predators and parasitoids to be more abundant, smaller in size, and more morphospecies rich in hayed grasslands, overall, there were no significant differences among wheat fields and hayed grasslands for predator and parasitoid abundance, biovolume, and morphospecies richness (Figures 1-3). The predator-prey ratio was greater in wheat (mean= 0.20, S.E.: 0.02) than in hayed grassland (mean= 0.13, S.E.: 0.02).

Minute Pirate Bugs (*Orius insidiosus*) were found at Niles (wheat: 8, hayed grassland: 6), Goessel (wheat: 4, hayed grassland: 4), Five Creeks (hayed grassland: 1), and Buckeye (hayed grassland: 2, wheat was not sampled). We collected four morphospecies of Coccinellids among all sites, and on average there was little difference in Coccinellid abundance between wheat and hayed grassland (mean in wheat: 2.25 S.E.: 0.9; mean in hayed grassland 2.8 S.E.: 0.08).

Overall, most of the predators and parasitoids in wheat were Hemipterans followed by Dipterans, Coleopterans, and Neuropterans (Figure 4). Among the Hemipterans collected in wheat, Nabids and predaceous Pentatomids (Asopinae) were most abundant and of substantial size. Most of the predators and parasitoids in hayed grassland were Hemipterans, Coleopterans, and Neuropterans (Figure 4). Among the Dipterans collected in hayed grasslands, flies of the family Dolichopodidae were most abundant. The orders with the greatest morphospecies richness were Hymenoptera (mean among hayed grasslands: 7.6 S.E. 1.2, wheat: 4.0 S.E. 1.4) and Hemiptera (mean among hayed grasslands: 2.2 S.E. 1.0, wheat: 2.5 S.E. 1.2).

### ***Pollinators***

Overall, there was significantly greater pollinator abundance, biovolume, and morphospecies richness in hayed grassland (Figures 1-3; Tables 1-3), and this pattern was consistent for all sites. Pollinators were collected in all of the hayed grasslands but in only one wheat field (Niles). Overall, most of the pollinators in hayed grasslands were Lepidopterans followed by Hymenopterans and Dipterans. Morphospecies richness was greatest for Lepidopterans and almost all of the morphospecies were Pyralids. There were three morphospecies of Hymenopteran pollinators, two of which were Halictids and one was Apidae.

### ***Detritivores***

There was significantly greater detritivore abundance and biovolume in hayed grassland (Tables 1 and 2; Figures 1 and 2). All of the detritivores were Dipterans and were mostly in the families Muscidae and Lauxaniidae. Detritivore morphospecies richness was significantly greater in hayed grassland than in wheat (Table 3; Figure 3).

## **Discussion**

Our results were not consistent with the prediction by the resource concentration hypothesis of denser plant stands supporting greater densities of herbivores. We found comparable densities of herbivores in hayed grasslands and wheat fields. However, we did find greater morphospecies richness, as expected due to greater host plant species richness, in hayed grasslands. We also found comparable abundance and morphospecies richness of predators and parasitoids among hayed grasslands and wheat fields which contradicted our expectation of observing greater predators and parasitoids in hayed grasslands based upon the enemies hypothesis. We expected to find greater detritivore and pollinator richness and abundance due to host plant richness and compositional effects (e.g. presence of flowering plants) and, we found greater detritivore and pollinator richness in hayed grasslands, as expected. Our hypotheses about insect functional group response to resource availability (through composition or biomass) in hayed grasslands are consistent with our results of greater pollinator and detritivore abundance, biovolume, and richness. Greater pollinator abundance, biovolume, and morphospecies richness in hayed grassland was likely due to the flowering plant species in the hayed grassland. In the wheat field there were no flowering plants when we sampled. However, there were flowering plants in the hayed grassland that would have attracted pollinators (Table 4). We also found greater detritivore abundance, biovolume, and richness in the hayed grassland. This is likely due to the lack of tillage (disturbance) in the hayed grassland. Without tillage, the hayed grassland



continued to have a source of food and plant cover through continuous crop residues and surface cover for detritivores (House and Stinner 1983; Doran et al. 1998; Wilson-Rummenie et al. 1999).

Our hypothesis was based upon specialist herbivores; in our samples we could have had a mix of specialist and generalist herbivores. For example, we found grasshoppers (Orthoptera; Figure 4), which are polyphagous and oligophagous, in both the hayed grasslands and wheat fields (Joern 1979; Joern 1983). Generalist herbivores are much less likely to be affected by plant community density or composition since they have a larger diet breadth. The presence of generalist herbivores could have resulted in our finding similar numbers of herbivores in hayed grassland and wheat fields. Herbivore control by parasitoids and predators was the same in hayed grasslands and wheat fields. However, herbivore species richness was greater in hayed grassland, which was likely due to compositional differences in the plant community in the hayed grassland (Table 4; Glover et al. 2010). The low overlap in the morphospecies found in both hayed grassland and wheat, suggests that spillover of insects from one production system to another is unlikely. It also suggests that the insects found in each production system are specific to that production system.

Our methodology of insect sampling, sweep sampling, was limited in that it provided only an estimate of insects that were active at the time of sampling and insects that could be caught by the sweep net. Insects that are nocturnal or ground-dwelling, such as carabids, may have been underestimated. Additionally, we sampled at only one time during the growing season. If we had sampled earlier in the spring when the wheat was photosynthetically active, then we may have found even more insects in the wheat. However, we chose to sample at the time when both production systems were at their maximum yield and about to be harvested. It is very unlikely

that the wheat fields had pesticide applied. The landowners did not report any pesticide applications and we found minute pirate bugs in wheat fields at Niles and Goessel. Minute pirate bugs are very sensitive to pesticide residues (Fauvel 1999). Another limitation of our methodology was identifying insect species to the level of morphospecies which did not allow us to distinguish between specialist and generalist herbivores. Information about herbivore specialization would have been useful in rejecting or accepting our original hypotheses.

Our results suggest at least two avenues for future research. One avenue for future research would be to address some of the methodological limitations of this study. For example, the data presented here are from one point in time and more information about and insights into the densities of insect functional groups could be gained. Furthermore, our morphospecies could be identified to species, which would provide further information about the diet breadth of herbivorous insects that we found in the hayed grasslands and wheat fields. Our use of sweep sampling placed a limitation on the insects we collected; sampling could be expanded to include nocturnal and ground or soil dwelling insects through pitfalling and soil bait trapping. Another direction for future research could be to examine the rates of herbivory and insect predation by insects in hayed grasslands and annual wheat fields. More specifically, we quantified insect abundance, morphospecies richness, and biovolume, but we did not examine plant yield/ biomass losses due to herbivores or rates of insect predation by insect predators and parasitoids. Some of the insects we collected could have been in the hayed grasslands or wheat fields without ever feeding on plants or insects. In order to examine rates of herbivory and predation, manipulations such as herbivore exclosure (e.g. insecticide or cages) or insect predator baiting (e.g. bait insect arrays or artificially increasing herbivorous insects) could provide insights into rates of insect herbivory and predation in hayed grasslands and wheat fields.

In conclusion, our results suggest that insects contribute to the ecosystem services that hayed grasslands provide. In contrast to annual wheat fields, hayed grasslands support insects that can provide pollination and decomposition services. However, grasslands and wheat fields support comparable numbers of herbivores and our results suggest that herbivore densities in grasslands are not any more limited by predators and parasitoids than herbivore densities in wheat fields. However, greater investigation into insect diet breadth and more intensive insect sampling of hayed grasslands and wheat fields could further our knowledge about the potential ecosystem service of insect herbivore control in these agroecosystems.

## Literature Cited

- Andow, D.A. 1991. Vegetational diversity and arthropod population response. *Annual Review of Entomology*. 36: 561-586.
- Colwell, R. K. 2013. *EstimateS*, Version 9.1: Statistical Estimation of Species Richness and Shared Species from Samples (Software and User's Guide). Freeware for Windows and Mac OS.
- Crews, T. E. 2005. Perennial crops and endogenous nutrient supplies. *Renewable Agriculture and Food Systems*. 20: 25-37.
- Crowder, D.W. and R. Jabbour. 2014. Relationships between biodiversity and biological control in agroecosystems: Current status and future challenges. *Biological Control*. 75: 8-17.
- Doran, J.W., E.T. Elliott, K. Paustian. 1998. Soil microbial activity, nitrogen cycling, and long-term changes in organic carbon pools as related to fallow tillage management. *Soil and Tillage Research*. 49: 3-18.
- Fauvel, G. 1999. Diversity of Heteroptera in agroecosystems: role of sustainability and bioindication. *Agriculture, Ecosystems, and Environment*. 74: 275-303.
- Glover, J.D., Culman, S.W., DuPont, S.T., Broussard, W., Young, L., Mangan, M., Mai, J., Crews, T.E., DeHaan, L.R., Buckley, D.H., Ferris, H., Reynolds, H., Turner, E., Wyse, D. 2010. Perennial grassland provides ecological benchmarks for agricultural sustainability. *Agriculture, Ecosystems and Environment* 137, p. 3-12.
- Hairston, N.G., F.E. Smith, L.B. Slobodkin. 1960. Community structure, population control, and competition. *American Naturalist*. 94: 421-425.
- House, G.J., B.R. Stinner. 1983. Arthropods in no-tillage soybean agroecosystems: Community composition and ecosystem interactions. *Environmental Management*. 7(1):23-28.
- Jackson, W. 1980. *New Roots for Agriculture*. University of Nebraska Press. Lincoln, Nebraska.
- Joern, A. 1979. Feeding Patterns in Grasshoppers (Orthoptera: Acrididae): Factors Influencing Diet Specialization. *Oecologia*. 38: 325-347.
- Joern, A. 1983. Host Plant Utilization by Grasshoppers (Orthoptera: acrididae) from a Sandhills Prairie. *Journal of Range Management*. 36 (6): 793-797.
- Klein, A., B. Vaissiere, J. Cane, I. Steffan-Dewenter, S. Cunningham, C. Kremen, T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proc Biol Sci*. 274(1608): 303-313.
- Letourneau, D.K. 1987. The enemies hypothesis: tritrophic interactions and vegetational diversity in tropical agroecosystems. *Ecology*. 68: 1616-1622.
- Magurran, A.E., 1988. *Ecological Diversity and Its Measurement*. Springer. Netherlands.
- Macfadyen, S., R. Gibson, A. Polaszek, R.J. Morris, P.G. Craze, R. Planque, W.O. Symondson, J. Memmott. 2009. Do differences in food web structure between organic and conventional farms affect the ecosystem service of pest control? *Ecology Letters*. 12: 229-238.

- Matson, P.A., W.J. Parton, A.G. Power. M.J.1997. Agricultural Intensification and Ecosystem Properties. *Science*. 277: 504-509.
- Pimentel, D., E. Terhune, R. Dyson-Hudson, S. Rochereau, R. Samis, E. Smith, D. Denman, D. Reifschneider, M. Shepard. 1976. Land Degradation: Effects on Food and Energy Resources. *Science*. 194 (4261): 149-155.
- Root, R.B. 1973. Organization of plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*. 43: 95-124.
- Salsbury, G.A. and S. C. White. 2000. *Insects in Kansas*. Kansas Dept. of Agriculture. Manhattan, Kansas.
- SPSS Inc. Released 2007. SPSS for Windows, Version 16.0. Chicago, SPSS Inc.
- Stiling, P., A.M. Rossi, and M.V. Cattell. 2003. Associational resistance mediated by natural enemies. *Ecological Entomology*. 28: 587-592.
- Triplehorn, C.A. and N. J. Johnson. 2004. Borror and DeLong's Introduction to the Study of Insects, 7<sup>th</sup> ed. Cengage Learning. Boston.
- Tylianakis, J.M., T. Tscharntke, O.T. Lewis. 2007. Habitat modification alters the structure of tropical host-parasitoid food webs. *Nature*. 445: 202-205.
- Wilson-Rummenie, A.C., B.J. Radford, L.N. Robertson, G.B. Simpson, and K.L. Bell. 1999. Reduced Tillage Increases Population Density of Soil Macrofauna in a Semiarid Environment in Central Queensland. *Environmental Entomology*: 28: 163-172.
- Weisser, W.W. and E. Siemann. 2004. The various effects of insects on ecosystem functioning *in* *Insects and Ecosystem Function*. Springer-Verlag. Berlin.

**Table 1**

Results of analysis of variance for number of insects collected.

		Number of Insects	Number of Herbivores	Number of Predators	Number of Pollinators	Number of Detritivores
Site	df	4,3	4,3	4,3	4,3	4,3
	F	0.34	1.34	6.26	0.78	5.46
	P	0.84	0.42	0.08	0.61	0.1
Agroecosystem	df	1,3	1,3	1,3	1,3	1,3
	F	3.42	0.72	0.06	<b>15.11</b>	<b>85.71</b>
	P	0.16	0.46	0.82	<b>0.03</b>	<b>0.003</b>

**Table 2**

Results of analysis of variance for insect biovolume.

		Insect Biovolume	Herbivore Biovolume	Predator Biovolume	Pollinator Biovolume	Detritivore Biovolume
Site	df	4,3	4,3	4,3	4,3	4,3
	F	2.35	0.59	4.94	0.46	3.00
	P	0.25	0.70	0.11	0.77	0.20
Agroecosystem	df	1,3	1,3	1,3	1,3	1,3
	F	0.10	1.11	1.27	<b>19.12</b>	<b>50.00</b>
	P	0.77	0.37	0.34	<b>0.02</b>	<b>0.01</b>

**Table 3**

Results of analysis of variance for insect morphospecies (morph.).

		Insect Morph.	Herbivore Morph.	Predator Morph.	Pollinator Morph.	Detritivore Morph.
Site	df	4,3	4,3	4,3	4,3	4,3
	F	1.75	7.43	1.07	0.42	0.51
	P	0.34	0.07	0.50	0.79	0.74
Agroecosystem	df	1,3	1,3	1,3	1,3	1,3
	F	<b>27.00</b>	<b>78.82</b>	5.02	<b>10.91</b>	<b>13.76</b>
	P	<b>0.01</b>	<b>&lt;0.01</b>	0.11	<b>0.05</b>	<b>0.03</b>

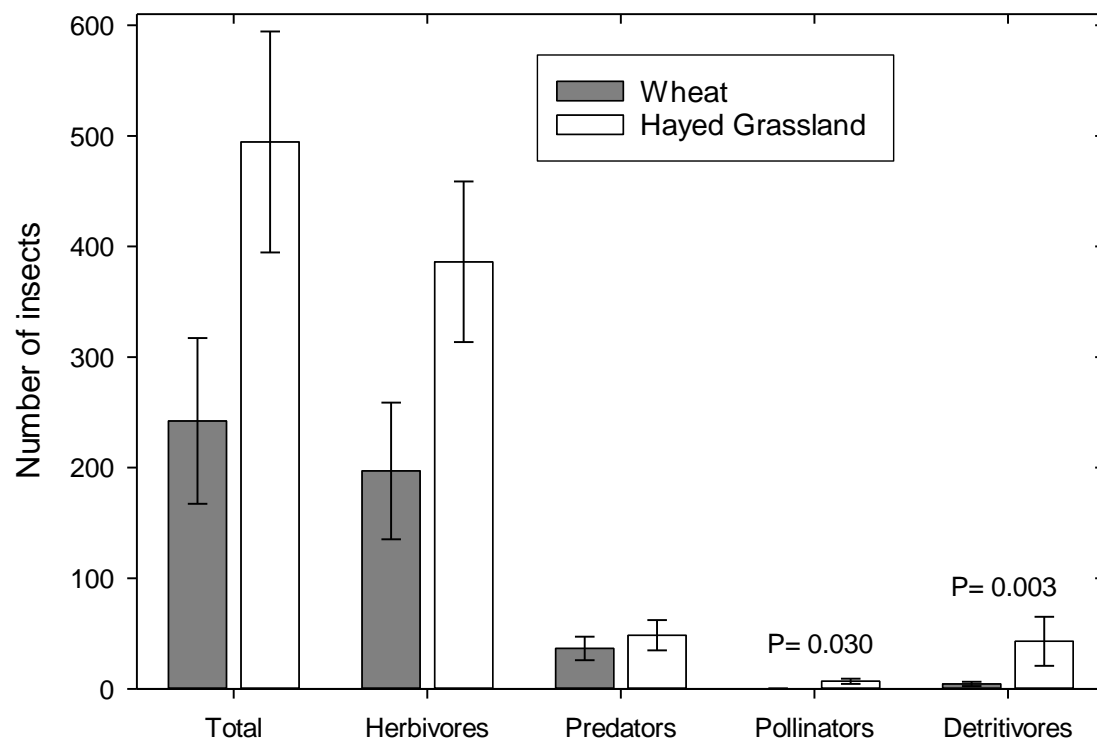


**Table 4**

Species of flowering plants present in hayed grassland at each site where insects were sampled. An “X” indicates presence of a flowering plant species at that site.

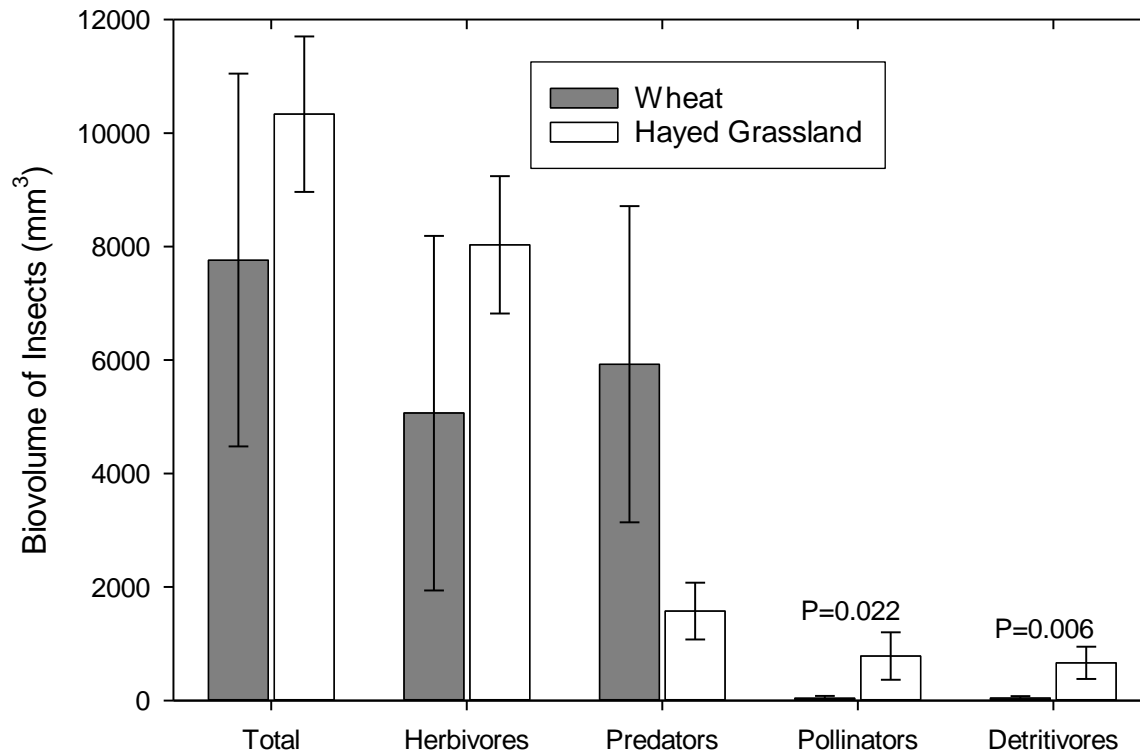
Species of Flowering Plant	Buckeye	Five Creek	Goessel	New Cambria	Niles
<i>Achillea millefolium lanulosa</i>	X				X
<i>Amorpha canescens</i>			X	X	X
<i>Artemesia ludoviciana</i>	X	X			
<i>Asclepias syriaca</i>			X		
<i>Asclepias verticillata</i>	X				X
<i>Asclepias viridis</i>	X		X		
<i>Aster ericoides</i>					X
<i>Baptisia australis</i>	X				X
<i>Callirhoe alceoides</i>			X	X	
<i>Callirhoe involucrata</i>	X	X		X	X
<i>Carex sp.</i>	X				
<i>Cirsium undulatum</i>			X	X	
<i>Conyza canadensis</i>	X	X			
<i>Coreopsis grandiflora</i>			X		
<i>Dalea candida</i>	X	X		X	X
<i>Desmanthus illinoensis</i>				X	
<i>Desmodium illinoense</i>		X		X	
<i>Erigeron annuus</i>	X	X	X	X	X
<i>Euphorbia chamaesyce</i>				X	
<i>Galium concinnum</i>	X		X		
<i>Geranium carolinianum</i>		X			
<i>Hieracium longipilum</i>	X				
<i>Kuhnia eupatorioides</i>				X	
<i>Lezpedeza capitata</i>		X			
<i>Linum sulcatum</i>		X	X		
<i>Lithospermum incisum</i>		X			
<i>Melilotus officinalis</i>	X				
<i>Oxalis stricta</i>	X		X	X	
<i>Physalis heterophylla</i>	X	X			
<i>Plantago sp.</i>	X	X	X	X	
<i>Potentilla arguta</i>	X				
<i>Psoralea argophylla</i>				X	X
<i>Psoralidium tenuiflorum</i>	X				
<i>Rosa arkansana</i>		X			
<i>Rudbeckia hirta</i>	X		X		X
<i>Salvia azurea</i>				X	X

<i>Schrankia nuttallii</i>					X
<i>Scutellaria lateriflora</i>			X		
<i>Silphium laciniatum</i>					X
<i>Sisymbrium officinale</i>	X		X		
<i>Stellaria media</i>			X		X
<i>Tragopogon dubius</i>	X	X	X		X
<i>Triodanis leptocarpa</i>	X	X	X		
<i>Triodanis perfoliata</i>			X	X	
<i>Vernonia baldwinii</i>					X
<i>Viola pubescens.</i>				X	
Total Flowering Plant Species Present:	22	15	18	16	16



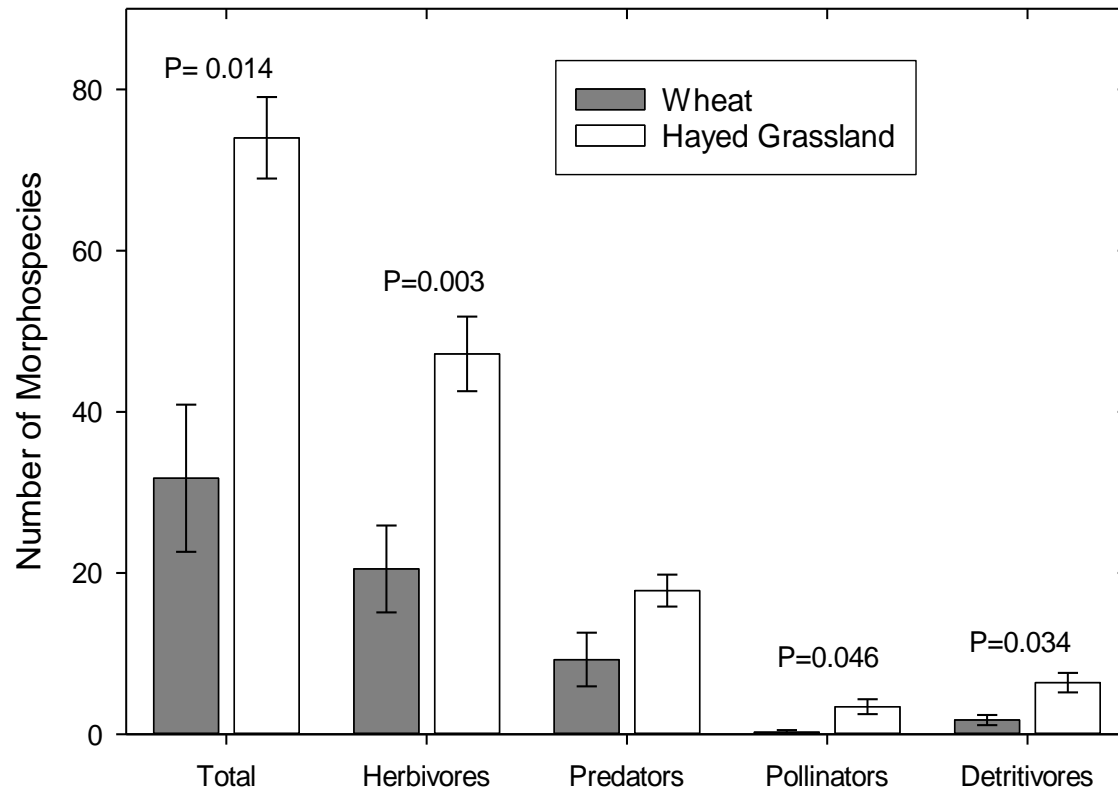
**Figure 1**

Abundance of insects collected from sweep net sampling in central Kansas wheat fields and hayed grasslands. Mean abundance for total insects and insect functional groups collected in wheat fields (n= 4) and hayed grasslands (n= 5). There were significantly fewer pollinators ( $P=0.030$ ) and detritivores ( $P=0.003$ ) found in wheat fields.



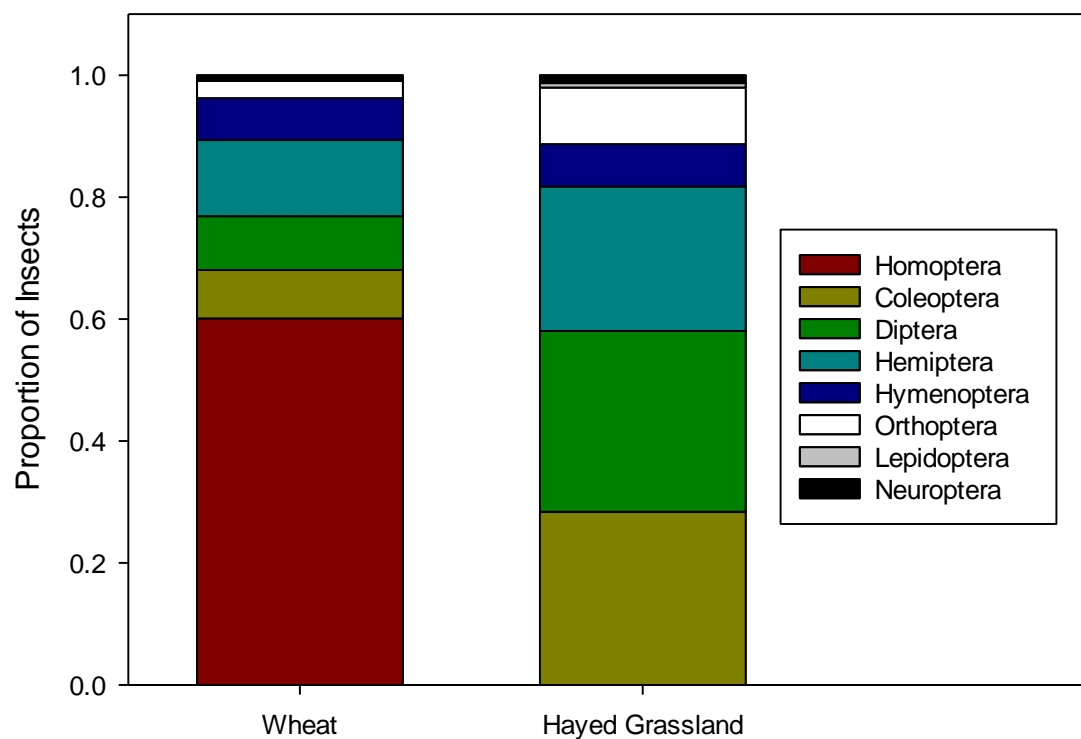
**Figure 2**

Biovolume of insects collected from sweep net sampling in central Kansas wheat fields and hayed grasslands. Insect biovolume, a measure of biomass, was estimated using cylindrical volume from insect length and thickness. Mean biovolume for all insects collected and insect functional groups. Significantly greater pollinator ( $P=0.022$ ) and detritivore ( $P=0.006$ ) biovolume was collected in hayed grasslands than in wheat fields.



**Figure 3**

Morphospecies richness found in sweep net samples collected in central Kansas wheat fields and hayed grasslands. Insect morphospecies richness for all insects collected and insect functional groups. There was greater morphospecies richness overall ( $P=0.014$ ) and for herbivores ( $P=0.003$ ), pollinators ( $P=0.046$ ), and detritivores ( $P=0.034$ ).



**Figure 4**

Proportion of insects by Order found in sweep net samples collected in central Kansas wheat fields or hayed grasslands. Proportionally, there were more Homopterans, Hemipterans, Orthopterans, and Neuropterans in the wheat fields than in the hayed grasslands. In hayed grasslands there were proportionally more Coleopterans, Dipterans, Hymenopterans, and Lepidopterans than were collected in the wheat fields.

**Title:** SURVEY OF INSECT HERBIVORY ON *DESMANTHUS ILLINOENSIS* AND  
LOCAL NEIGHBORHOOD DENSITY IN THREE PRAIRIE SITES

**Abstract**

*Desmanthus illinoensis*, Illinois Bundleflower, is an herbaceous perennial legume that is in the early stages of domestication as a perennial grain crop. The coleopteran *Anomoea flavokansiensis* has a limited diet breadth and our observation was that this species was the primary insect herbivore of *D. illinoensis* in natural grasslands in Kansas. Selective grazing, by a plant herbivore such as *A. flavokansiensis*, may arise from local plant neighborhood heterogeneity which can affect the frequency and intensity of insect herbivore feeding and abundance. For three years, we examined insect herbivory on *D. illinoensis* in three prairie grasslands in central Kansas using herbivore exclosure/reduction to examine leaf herbivory by insects on *D. illinoensis* and the effect of herbivory on seed head maturation. We examined the influence of local legume density and grass density on *D. illinoensis* herbivory by quantifying legume and grass cover within 1m<sup>2</sup> around the experimental plant. During all three years there was a significant effect of insect exclosure; there was greater leaf herbivory without insecticide. However, with a reductions in leaf herbivory there was not an increase in seed head maturation. There was no relationship between foliar herbivory of *D. illinoensis* and legume cover around the experimental plant. However, we observed reduced foliar herbivory on the experimental *D. illinoensis* with more grass cover suggesting that grasses provide associational resistance to herbivory for *D. illinoensis*. We observed the resilience of *D. illinoensis* to foliar herbivory in our experiment; reducing foliar herbivory on *D. illinoensis* did not increase rates of seed head maturation. However, if *A. flavokansiensis* reduces yield in production systems with *D.*

*illinoensis* then yield losses could be reduced by growing *D. illinoensis* in polyculture with grasses.

## **Introduction**

Perennial grain production systems have been proposed to resemble prairie ecosystems and thus could be a unique intersection between ecology and agroecology (Jackson and Jackson 1999). Using prairie ecosystems as a model, perennial grain production systems are designed as polycultures (DeHaan et al. 2005) with legumes playing an important role to meet the nitrogen requirements of the polyculture (Crews 2005). A suggested advantage of perennial grain cropping systems over annual grain cropping systems is a greater resilience to pests through perennial plant life history traits such as greater investment in plant defenses and through reductions in herbivore abundance (Cox et al. 2006, Cox et al. 2010). Reductions in yield losses from insect herbivores in perennial polycultures could arise from one crop in the polyculture providing associational resistance to another crop in the polyculture through a process of associational resistance (Root 1973).

*Desmanthus illinoensis*, Illinois Bundleflower, is an herbaceous perennial legume that is in the early stages of domestication as a perennial grain crop (DeHaan et al. 2005, Cox et al. 2006, Glover et al. 2007, Cox et al. 2010). There is particular interest in *D. illinoensis* because it can produce many large seeds and is a good nitrogen fixer (Cox et al. 2010). The range of *D. illinoensis* is from central North America to the east coast and it is commonly found in small scattered stands in disturbed areas (Latting 1961).



Leaf herbivory on *D. illinoensis* by *Anomoea flavokansiensis* (Coleoptera: Chrysomelidae) has been documented (Latting 1961, Stiefel and Margolies 1997) and Latting (1961) observed that *A. flavokansiensis* leaf herbivory resulted in initiated seed heads not maturing to set seed. *Anomoea flavokansiensis* has a limited diet breadth of *D. illinoensis* (Stiefel and Margolies 1997) and our preliminary observation was that this species was the primary insect herbivore of *D. illinoensis* in natural grasslands in Kansas. It is therefore possible that *A. flavokansiensis* could reduce seed yield of *D. illinoensis* when it is in a perennial cropping system. In polyculture, the presence of *D. illinoensis* has been found to increase yield (above-ground biomass or seed production) of some neighboring grass species, which suggests that *D. illinoensis* could be an important component of a perennial cropping system (Dovel et al. 1990, Piper 1993, Posler et al. 1993, Springer et al. 2001). However, *D. illinoensis*- insect interactions in polyculture (grasslands) are less well known.

Insect herbivores are known to influence the structure and composition of plant communities through selective grazing and subsequent changes in plant physiology, growth, and population dynamics (Huntly 1991, Tschardtke and Greiler 1995, Carson and Root 1999, 2000, Maron et al. 2002, Weisser and Siemann 2004). Selective grazing may arise from local plant neighborhood heterogeneity which can affect the frequency and intensity of insect herbivore feeding and abundance (Stanton 1983, Andow 1991). In a process known as associational resistance or associational defense, some plants may experience less herbivory when co-occurring with heterospecific neighbors than in monoculture (Tahvanainen and Root 1972, Root 1973, Morrow et al. 1989). In contrast, some plant hosts may experience associational susceptibility, or more herbivory, when in the presence of conspecifics (Parker and Root 1981; Rand 2003; White and Whitham 2000; Agrawal 2004). Andow (1991) reviewed 209 studies on 287 arthropod species

in mono- and polyculture and found that insect population densities were less in polyculture for 51.9% of insect species (support for associational resistance) and greater in polyculture for 15.3% of insect species (support for associational susceptibility). However, whether plant neighbors provide associational resistance or susceptibility may rely heavily on insect herbivore diet breadth. Among monophagous herbivore species 59.1% had lesser population densities in polyculture versus 28.4% among polyphagous herbivore species. In fact, among polyphagous herbivore species studied, 40.3% had greater population densities in polyculture vs. 7.7% for monophagous species. Thus, plant neighbors in polyculture are likely to provide associational resistance from monophagous insect herbivores while associational susceptibility for polyphagous insect herbivores.

Here, we seek to examine insect herbivory on *D. illinoensis* in pasture and prairie grassland in central Kansas. Given that *D. illinoensis* could be a valuable component of perennial polycultures and *D. illinoensis* has a monophagous insect herbivore, we seek to examine if there is an effect of associational resistance for *D. illinoensis* in prairie that could be useful in informing perennial polyculture design. We used herbivore exclosure/reduction to examine leaf herbivory by insects on *D. illinoensis* and the effect of herbivory on seed head maturation. Previous observation by Latting (1961) suggests that foliar herbivory on *D. illinoensis* can result in fewer matured seed heads. In our experiment, we expected to see greater seed head maturation with herbivore exclosure/reduction. We also examined the influence of the existing plant neighborhood on herbivory of *D. illinoensis*. We expected the sole insect herbivore of *D. illinoensis* to be *A. flavokansiensis*, which has a narrow diet breadth. Based on associational resistance theory, we therefore expected to see lower herbivory on *D. illinoensis* plants as neighbor diversity increased.

## Methods

During 6-7 June 2006, 27 *D. illinoensis* plants that were at least 3 m apart were arbitrarily selected at three sites southeast of Salina in Saline County, Kansas, USA. These three sites were used because they represent common prairie grassland communities in central Kansas and there was abundant *Desmanthus illinoensis*. Plants were labeled using numbered aluminum tags and pin flags for later re-location.

The sites were: Waub Prairie (38.46N, 97.34W), Haig Prairie (38.47N, 97.33W), and Van Tassel Pasture (38.46N, 97.34W). Waub Prairie was a never tilled upland prairie dominated by *Andropogon gerardii*, *Sorghastrum nutans*, *Bouteloua curtipendula*, *Panicum virgatum*, and *Amorpha canescens*. Haig Prairie was a wash area with exposed substrate and the vegetation was dominated by *Bouteloua curtipendula* and *Stipa spartea*. Van Tassel Pasture was pasture but was fallow for at least five years prior to application of the treatments and was dominated by *Bromus tectorum* and *D. illinoensis*.

The 27 plants at each site were randomly assigned to an aqueous insecticide treatment, water-only control, and untreated control (9 plants per treatment and each control). The insecticide was cyfluthrin (concentration 0.52mL/ L in water) and is in the same family of insecticides that has been previously used successfully in insect exclusion studies without evidence of secondary effects (Carson and Root 1999; Root 1996; Siemann et al. 2004). Insecticide and water controls were applied at the initiation of the experiment and then every two weeks afterwards or after a rainfall until the plants were harvested during 24-26 August 2006. There were six total applications of water or insecticide. For the initial two applications, 35 mL of water or insecticide in water were applied per plant. For the four subsequent applications, the *D. illinoensis* plants were larger and 70 mL of water or insecticide in water were applied.

Insecticide or water was applied between 7 and 9 PM to minimize potential for interactions of heat with the insecticide and/or burning due to water droplets. During 2007 and 2008, the insecticide and water controls were initiated in June (8 June 2007 and 11 June 2008) using the same protocol as the previous year with six total applications until the plants were harvested in August (12-26 August 2007 and 18-25 August 2008). At the beginning of each growing season initial measurements of plant height and number of leaves were made on the experimental *D. illinoensis* plants. In August of 2006, 2007, and 2008, measures of *D. illinoensis* number of leaves, number of damaged leaves, number of matured seed heads, and number of initiated seed heads were made to examine for treatment differences. In August for all three years, plant cover around each *D. illinoensis* plant was visually estimated using a 1m<sup>2</sup> quad placed with the experimental plant in the middle.

Analysis of variance (ANOVA) was performed using SPSS 21 and was used to examine effects of site (random) and insect exclosure (fixed) and a covariate (initial height or initial number of leaves) on *D. illinoensis* number of leaves, number of seed heads initiated, proportion of leaves damaged (number of damaged leaves/ total number of leaves), and proportion of seed heads matured (number of mature heads/ total number of seed heads). Not all *D. illinoensis* plants emerged every year; within our experiment we had 81 plants and 25 plants were dormant for at least one year. Because of the large proportion of plants that did not grow every year of our experiment, we were unable to examine year in our statistical model (e.g. repeated measures ANOVA). Three, separate analyses for each year (2006, 2007, and 2008) were performed. Data for number of leaves and total seed heads were transformed ( $\sqrt{y+0.5}$ ) to conform to assumptions of normality. Data for proportion of leaves damaged and proportion of seed heads matured were

transformed ( $\arcsin \sqrt{p}$ ) to conform to assumptions of normality. For number of leaves and proportion of leaves damaged, we used initial number of leaves as a covariate. For number of seed heads initiated and proportion of seed heads matured, we used initial height as covariate. Regression analysis was performed to examine the effects of plant neighborhood (plant species richness, proportion of legume cover, proportion of forb cover, or proportion of grass cover/ m<sup>2</sup>) on herbivory (proportion of leaves damaged on plants with nothing applied). All of the legumes in the plant neighborhoods that we quantified were *D. illinoensis*. Other species of legumes were not present in any of the plant neighborhoods that we quantified.

## **Results**

### ***Survivorship***

While all of the nine replicate *Desmanthus illinoensis* plants for each treatment and site survived until harvest in August, 2006, not all of the plants re-emerged the subsequent year. Most of the plants that did not re-emerge in 2007 were at Van Tassel Pasture (number that did not emerge: 3 plants in untreated controls; 4 plants in water controls; and 4 plants in insecticide treatment). At Haig Prairie, two plants in the water control did not emerge and, at Waub Prairie one plant in the untreated control did not emerge. All of the plants that emerged in 2007 survived until harvest. In 2008, more plants did not re-emerge. Emergence was low at two sites: Haig Prairie (number that did not emerge: 3 plants in untreated control; 4 plants in water only control; and 2 plants in insecticide treatment) and Van Tassel Pasture (number that did not emerge: 2 plants in untreated control; 2 plants in water only control; and 1 plant in insecticide treatment). At Waub Prairie, one plant in the untreated control and two plants in the insecticide treatment did not re-emerge. All of the plants that emerged in 2008 survived until harvest.

### ***Vegetative and reproductive responses***

Overall, by the end of the growing season in 2006, *D. illinoensis* plants had on average 26.5 (SE 2.9) leaves, 8.3 (SE 1.6) seed heads, and 32% (SE 4) of seed heads matured. There were no significant effects of insecticide or the interaction of insecticide and site on number of *D. illinoensis* leaves ( $P > 0.9$ ), total number of seed heads, or proportion of matured seed heads (Table 1). There was a significant effect of site on number of leaves, proportion of leaves damaged, and proportion of matured seed heads (Table 1). There was a significant effect of site for number of leaves because *D. illinoensis* plants had more leaves at Haig prairie (45.1, SE 7) than at Van Tassel pasture (16.4, SE 1.9) and Waub prairie (17.9, SE 1.9). There was also a significant effect of site for proportion of seed heads matured; *D. illinoensis* plants at Van Tassel pasture had lesser seed head maturation (proportion seed heads matured: 2%, SE 2) than at Haig prairie (proportion seed heads matured: 50%, SE 7) and Waub prairie (proportion seed heads matured: 44%, SE 8).

There were significant effects of insecticide treatment and site on the proportion of leaves damaged in 2006 (Table 1). For all sites, on average, plants with insecticide had lesser rates of leaf herbivory (insecticide treatment 53%, SE 7; untreated control 83%, SE 4; water only control 85%, SE 5; Figure 1). There was also an effect of site on the proportion of leaves damaged in 2006; the *D. illinoensis* plants at Haig prairie (47%, SE 6) had lesser rates of leaf herbivory than *D. illinoensis* plants at Van Tassel pasture (91%, SE 3) and Waub prairie (83%, SE 5).

Overall in 2007, on average, plants had 36.3 (SE 2.8) leaves, 16.7 (SE 2.6) seed heads, and 67% (SE 4) of the seed heads matured. In 2007 we found a significant effect of site for the proportion of seed heads matured and number of seed heads initiated (Table 2). At Haig in 2007, more *D. illinoensis* seed heads were initiated (24.28 seed heads, SE 5.83) than at Waub (14.00 seed heads, SE 3.23) or Van Tassel (9.38, SE 2.44). At Van Tassel in 2007, proportionally fewer seed heads

matured (43%, SE 9) than at Waub (81%, SE 6) and Haig (69%, SE 6). There was no effect of herbivore enclosure or site for the number of leaves at harvest (Table 2). In 2007, we did not find an interactive effect of site and herbivore enclosure for number of leaves, proportion of leaves damaged, proportion of heads matured, or number of seed heads initiated (Table 2).

Overall in 2008, on average, plants had 29.5 (SE 2.3) leaves, 13.2 (SE 2.6) seed heads, and 23% (SE 3) of seed heads matured. There was no effect of herbivore enclosure for number of leaves, proportion of seed heads matured, or number of seed heads initiated (Table 3). There was no effect of site for proportion of leaves damaged or number of seed heads initiated (Table 3); there was an effect of site on the number of leaves of *D. illinoensis* plants and proportion of seed heads matured (Table 3). In 2008 at Haig, plants had more leaves (37.56, SE 5.97) than at Waub (27.83, SE 2.82) or Van Tassel (23.56, SE 2.70). Proportionally, fewer seed heads matured at Van Tassel (13%, SE 4) than at Waub (25%, SE 5) or Haig (32%, SE 5). There were no significant interactive effects of herbivore enclosure and site (Table 3).

During 2007 and 2008, there was a significant effect of insecticide on the proportion of leaves damaged (Tables 2 and 3). Leaf herbivory rates in 2007 and 2008 were reduced by at least 56% by the insecticide treatment (proportion of leaves damaged: 2007-insecticide treatment 10%, SE 1; untreated control 40%, SE 5; water only control 40%, SE 6; 2008- insecticide treatment 16%, SE 3; untreated control 56%, SE 7; water only control 54%, SE 6; Figures 2 and 3)

### ***Plant neighborhood***

*Desmanthus illinoensis* cover was very low (Table 4) around the experimental plants. There was no relationship between legume cover in the plant neighborhood and herbivory of *D. illinoensis* for all three years (Table 4). However, there was a strong relationship between grass cover in the

plant neighborhood and herbivory of *D. illinoensis* for all three years (Table 4, Figure 4). There was less foliar herbivory of *D. illinoensis* with more grass cover for all three years. There was grass cover in all of the neighborhoods (2006: 30-75% cover; 2007: 40-70% cover; 2008: 50-80% cover). There was no relationship between foliar herbivory and plant neighborhood species richness, forb cover, or grass species richness (Table 4). At Waub we found five forb species and five grass species (Table 5). At Haig we found seven forb species and four grass species (Table 5). At Van Tassel we found four forb species and two grass species (Table 5).

## Discussion

For all three years, we found significant rates of foliar herbivory on *Desmanthus illinoensis* and foliar herbivory was less when the experimental *Desmanthus illinoensis* plant was in a plant neighborhood with greater grass cover. With herbivore exclosure/ reduction, we were able to reduce rates of foliar insect herbivory by at least half. However, these reductions in foliar herbivory did not mean greater seed head maturation. This was unexpected due to the observation by Latting (1961) of foliar feeding by *Anomoea flavokansiensis* reducing seed head maturation and the high densities of *A. flavokansiensis* on our experimental plants (personal observation). This result could be due to the perenniality of *D. illinoensis*. The plants in the experiment were already established and may have had the ability to overcome foliar feeding losses, resulting in no change in rates of seed head maturation despite leaf herbivory.

We observed the greatest rates of foliar herbivory in 2006, which was the year with the least precipitation during the experiment (National Weather Service 2014). Also during 2006, the plants were smaller (fewer leaves) and produced fewer seed heads than in the subsequent two years. Less precipitation in 2006 could have resulted in *D. illinoensis* plants with fewer leaves and seed heads. *Anomoea flavokansiensis* has been observed to have a narrow diet breadth



(Stiefel and Margolies 1997). If there was less plant tissue available to *A. flavokansiensis* (i.e. plants had fewer leaves during 2006) then there may have been greater foliar herbivory per plant. Alternately, the droughty conditions could have made the plant more attractive to herbivores through changed palatability of the plant and/ or if there were fewer available plant defenses. The plant stress hypothesis predicts that plants which are physiologically stressed will be more attractive and beneficial to herbivores (White 1969, 1970, 1984; Mattson and Haack 1987). This hypothesis predicts a non-linear relationship between host plant suitability for herbivorous insects, where host plant suitability at first increases with greater stress and then decreases with extreme, severe, and prolonged stress that is likely to be debilitating to the plant (Mattson and Haack 1987). Stressed plants can be more suitable to herbivores due to elevated plant nutrient levels such as nitrogen (White 1969, 1984; Mattson and Haack 1987) and soluble carbohydrate (Mattson and Haack 1987; Louda and Collinge 1992). In our experiment during 2006, conditions were dry but there was not an extreme drought. Therefore, the *D. illinoensis* plants in our experiment would be predicted by the plant stress hypothesis to have been more suitable to insect herbivores during 2006 than during the subsequent years when there was greater precipitation.

We also observed that not all of the plants re-emerged every year. At initiation of the experiment we had 81 plants and in the succeeding two years there were 25 plants that had a period of dormancy (1-2 yrs). Three of the plants that did not emerge in 2007, did emerge in 2008. This suggests that *D. illinoensis*, while perennial and polycarpic, may have periods of dormancy.

There was no relationship between foliar herbivory and cover of *D. illinoensis* within the plant neighborhood of the experimental plants. Over 80% of the experimental plants did not have cover of other *D. illinoensis* plants (or other legumes) within their neighborhood and therefore

our experiment could only weakly evaluate associational susceptibility conferred by neighboring *D. illinoensis* plants. We found a significant relationship between *D. illinoensis* foliar herbivory and grass cover within the plant neighborhood of the experimental plants. There was less *D.illinoensis* foliar herbivory with greater grass cover suggesting that grasses in the neighborhood of the experimental plants conferred associational resistance to the experimental *D. illinoensis* plants. The resource concentration hypothesis proposes at least three mechanisms underlying how conspecifics and heterospecifics can alter insect herbivory. First, one host plant may emit volatile compounds that interfere with the search behavior of an insect herbivore of another host plant (Stanton 1983). Second, with lessening density and greater diversity of host plants, distance among hosts increases and apparency may decrease (Root 1973, Rausher 1981). Third, a less palatable host plant may repel insect herbivores altogether (Tahvanianen and Root 1973) or a more palatable host plant may divert insect herbivores away from another host plant (Atsatt and O'Dowd 1976). In our experiment, it is likely that apparency and palatability affected the associational resistance conferred by grasses on *D. illinoensis* plants. Grass cover may have affected apparency in that often the grasses were taller than the *D. illinoensis* plant (personal observation) and grass cover may have affected search behavior by *A. flavokansiensis*. Additionally, the narrow diet breadth of *A. flavokansiensis* means that grasses are likely to not be palatable to the insect. With greater grass cover, there was possibly less palatable biomass apparent to *A. flavokansiensis*.

Results from our experiment suggest there are at least three future directions of research. We made an observation that could be challenging for future breeding programs of *D. illinoensis*. *Desmanthus illinoensis* can be dormant for a growing season; within a production system there could be a significant loss in yield if there are dormant plants within one growing season. Thus,

an examination of the mechanisms of *D. illinoensis* dormancy could be informative for future *D. illinoensis* breeding programs and inclusion in perennial polycultures. For example, if dormancy traits persist in *D. illinoensis* then it would be useful to know if perennial polyculture design could be changed to minimize dormancy and subsequent yield losses. Another future avenue for research would be to investigate the size of the neighborhood (grass cover) on herbivory of *D. illinoensis*. Our neighborhoods were at the scale of 1 m<sup>2</sup>, but grass cover more locally (e.g. 0.5 m<sup>2</sup>) could be as effective. Lastly, due to the low densities of *D. illinoensis* plants in the neighborhoods of our experimental plants we were not able to do a very robust test of associational susceptibility. Plant neighborhoods could be experimentally manipulated (e.g. placement of potted *D. illinoensis* plants near a focal/ experimental *D. illinoensis* plant) to examine for associational susceptibility. We observed the resilience of *D. illinoensis* to foliar herbivory in our experiment; reducing foliar herbivory on *D. illinoensis* did not increase rates of seed head maturation. However, if foliar herbivory affects the productivity of the production system (e.g. through reduced seed yield or biomass for forage) then losses from foliar herbivory on *D. illinoensis* could be reduced by including grasses within the perennial polyculture.

## Literature Cited

- Agrawal, A.A. 2004. Resistance and Susceptibility of Milkweed: Competition, Root Herbivory, and Plant Genetic Variation. *Ecology*. 85: 2118-2133.
- Andow, D.A. 1991. Vegetational diversity and arthropod population response. *Annual Review of Entomology*. 36: 561-586.
- Carson, W.P. and R. Root. 2000. Herbivory and plant species coexistence: community regulation by an outbreaking phytophagous insect. *Ecological Monographs*. 70:73-99.
- Carson, W.P. and R. Root. 1999. Top-down effects of insect herbivores during early succession: influence on biomass and plant dominance. *Oecologia* 121:260-272.
- Cox, T.S., J.D. Glover, D.L. Van Tassel, C.M. Cox, and L.R. DeHaan. 2006. Prospects for developing perennial grain crops. 2006. *BioScience*. 56: 649-659.
- Cox, T.S., D.L. Van Tassel, C.M. Cox, L.R. Dehaan. 2010. Progress in breeding perennial grains. *Crop & Pasture Science*. 61: 513-521.
- Crews, T. E. 2005. Perennial crops and endogenous nutrient supplies. *Renewable Agriculture and Food Systems*. 20: 25-37.
- DeHaan, L.R., D.L. Van Tassel, T.S. Cox. 2005. Perennial grain crops: A synthesis of ecology and plant breeding. *Renewable Agriculture and Food Systems*. 20: 5-14.
- Dovel, R.L., M.A. Hussey, and E.C. Holt. 1990. Establishment and survival of Illinois bundleflower interseeded into and established Kleingrass pasture. *Journal of Range Management*. 53: 153-156.
- Glover, J.D., C.M. Cox, and J.P. Reganold. 2007. Future Farming: A Return to Roots? *Scientific American*. p. 82-89.
- Huntly, N. 1991. Herbivores and the dynamics of communities and ecosystems. *Annual Review of Ecology and Systematics*. 22: 477-503.
- Jackson, W. and L.L. Jackson. 1999. Developing high seed yielding perennial polycultures as a mimic of mid-grass prairie in Agriculture as a Mimic of Natural Ecosystems. Kluwer. Dordrecht, The Netherlands.
- Latting, J. 1961. The Biology of *Desmanthus illinoensis*. *Ecology*. 43: 48-493.
- Louda, S.M. and S.K. Collinge. Plant resistance to insect herbivores: a field test of the environmental stress hypothesis. *Ecology*. 73(1): 153-169.
- Mattson, W.J. and R.A. Haack. 1987. The role of drought in outbreaks of plant-eating insects. *Bioscience*. 37(2): 110-118.
- Maron, J.L., J.K Combs, and S.M. Louda. 2002. Convergent demographic effects of insect attack on related thistles in coastal vs. continental dunes. *Ecology*. 83: 3382-3392.
- Morrow, P.A., D.W. Tonkyn, and R.J. Goldburg. 1989. Patch colonization by *Trirhabda Canadensis* (Coleoptera, Chrysomelidae): Effects of plant species composition and wind. *Oecologia*. 81: 43-50.

- National Weather Service. Annual Precipitation and Snowfall Records for Wichita Kansas. ICT Webmaster, 14 February 2014. 17 November 2014.
- Parker, M.A. and R.B. Root. 1981. Insect herbivores limit habitat distribution of a native composite, *Machaeranthera canescens*. *Ecology*. 62: 1390-1392.
- Piper, J.K. 1993. Neighborhood effects on growth, seed yield, and weed biomass for three perennial grains in polyculture. *Journal of Sustainable Agriculture*. 4: 11-31.
- Posler, G.L., A.W. Lenssen, and G.L. Fine. 1993. Forage yield, quality, compatibility, and persistence of warm-season grass-legume mixtures. *Agronomy Journal*. 85: 554-560.
- Rand, T.A. 2003. Herbivore-mediated apparent competition between two salt marsh forbs. *Ecology*. 84: 1517-1526.
- Root, R. 1973. Organization of plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*. 43: 95-124.
- Root, R. 1996. Herbivore pressure on goldenrods (*Solidago altissima*): its variation and cumulative effects. *Ecology*. 77:1074-1087.
- Siemann, E., W.P. Carson, W.E. Rogers, and W.W. Weisser. 2004. Reducing herbivory using insecticides in *Insects and Ecosystem Function*. Springer-Verlag. Berlin.
- Springer, T.L., G.E. Aiken, and R.W. McNew. 2001. Combining ability of binary mixtures of native, warm-season grasses and legumes. *Crop Science*. 41: 818-823.
- Stanton, M.L. 1983. *Spatial Patterns in the Plant Community and Their Effects upon Insect Search in Herbivorous Insects*. Academic Press. New York.
- Stiefel, V.L., D.C. Margolies. 1998. Is hosts plant choice by a clytrine leaf beetle mediated through interactions with the ant *Crematogaster lineolate*? *Oecologia*. 115: 434-438.
- Tahavanainen, J.O. and R.B. Root. 1972. The influence of vegetational diversity on the population ecology of a specialized herbivore, *Phyllotreta cruciferae* (Coleoptera: Chrysomelidae). *Oecologia*. 10: 321-346.
- Tscharntke, T. and H. Greiler. 1995. Insect communities, grasses, and grasslands. *Annual Review of Entomology*. 40: 535-558.
- Weisser, W.W. and E. Siemann. 2004. The various effects of insects on ecosystem functioning in *Insects and Ecosystem Function*. Springer-Verlag. Berlin.
- White, T.C.R. 1969. An index to measure weather-induced stress of trees associated with outbreaks of psyllids in Australia. *Ecology*. 50: 905-909.
- White, T.C.R. 1970. The nymphal stage of *Cardiaspina densitexta* (Homoptera: Psyllidae) on leaves of *Eucalyptus fasciculosa*. *Australian Journal of Zoology*. 18: 272-293.
- White, T.C.R. 1984. The abundance of invertebrate herbivores in relation to the availability of nitrogen in stressed food plants. *Oecologia*. 63: 90-105.
- White, J.A. and T.G. Whitham. 2000. Associational susceptibility of cottonwood to a box elder herbivore. *Ecology*. 81: 1795-1803.

**Table 1**

Analysis of variance results for 2006. For number of leaves and proportion of leaves damaged at harvest, a covariate of initial number of leaves was used. For proportion of seed heads matured and total seed heads initiated at harvest, a covariate of initial plant height was used.

		Number of Leaves	Proportion of Leaves Damaged	Proportion of Heads Matured	Total Seed Heads Initiated
Covariate -- Number of Leaves	df	1, 71	1, 71	-	-
	F	<b>36.99</b>	0.91	-	-
	P	<b>&lt;0.01</b>	0.34	-	-
Covariate -- Height	df	-	-	1, 71	1, 71
	F	-	-	0.52	<b>22.48</b>
	P	-	-	0.48	<b>&lt;0.01</b>
Herbivore Exclosure	df	2, 4.3	2, 4.2	2, 4.6	2, 4.1
	F	1.25	<b>12.3</b>	2.79	0.66
	P	0.37	<b>0.02</b>	0.16	0.56
Site	df	2, 5	2, 4.7	2, 10.6	2, 4.7
	F	<b>8.68</b>	<b>23.79</b>	<b>41.73</b>	7.11
	P	<b>0.02</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>	0.37
Herbivore Exclosure x Site	df	4, 71	4, 71	4, 71	4, 71
	F	1.074	1.399	0.293	2.133
	P	0.38	0.24	0.88	0.09

**Table 2**

Analysis of variance results for 2007. For number of leaves and proportion of leaves damaged at harvest, a covariate of initial number of leaves was used. For proportion of seed heads matured and total seed heads initiated at harvest, a covariate of initial plant height was used.

		Number of Leaves	Proportion of Leaves Damaged	Proportion of Heads Matured	Total Seed Heads Initiated
Covariate -- Number of Leaves	df	1, 56	1, 56	-	-
	F	<b>14.16</b>	0.027	-	-
	P	<b>&lt;0.01</b>	0.87	-	-
Covariate -- Height	df	-	-	1, 56	1, 56
	F	-	-	<b>7.07</b>	<b>13.45</b>
	P	-	-	<b>0.01</b>	<b>&lt;0.01</b>
Herbivore Exclosure	df	2, 5.1	2, 4.9	2, 4.5	2, 5.6
	F	0.17	<b>13.89</b>	1.56	0.92
	P	0.85	<b>0.01</b>	0.306	0.45
Site	df	2, 4.4	2, 4.3	2, 4.1	2, 4.3
	F	2.15	1.97	<b>7.12</b>	<b>10.33</b>
	P	0.22	0.25	<b>0.05</b>	<b>0.02</b>
Herbivore Exclosure x Site	df	4, 56	4, 56	4, 56	4, 56
	F	0.73	0.95	1.19	0.38
	P	0.58	0.44	0.33	0.82

**Table 3**

Analysis of variance results for 2008. For number of leaves and proportion of leaves damaged at harvest, a covariate of initial number of leaves was used. For proportion of seed heads matured and total seed heads initiated at harvest, a covariate of initial plant height was used.

		Number of Leaves	Proportion of Leaves Damaged	Proportion of Heads Matured	Total Seed Heads Initiated
Covariate -- Number of Leaves	df	1, 50	1, 50	-	-
	F	<b>30.74</b>	1.77	-	-
	P	<b>&lt;0.01</b>	0.19	-	-
Covariate -- Height	df	-	-	1, 50	1, 50
	F	-	-	<b>23.73</b>	<b>9.15</b>
	P	-	-	<b>&lt;0.01</b>	<b>&lt;0.01</b>
Herbivore Exclosure	df	2, 4.4	2, 4.3	2, 4.1	2, 4.1
	F	0.56	<b>10.6</b>	1.64	5.14
	P	0.61	<b>0.02</b>	0.3	0.08
Site	df	2, 4.8	2, 4.6	2, 4.7	2, 5.8
	F	<b>6.00</b>	1.04	<b>9.50</b>	3.22
	P	<b>0.05</b>	0.42	<b>0.02</b>	0.13
Herbivore Exclosure x Site	df	4, 50	4, 50	4, 50	4, 50
	F	0.89	1.08	0.85	2.02
	P	0.48	0.38	0.50	0.11



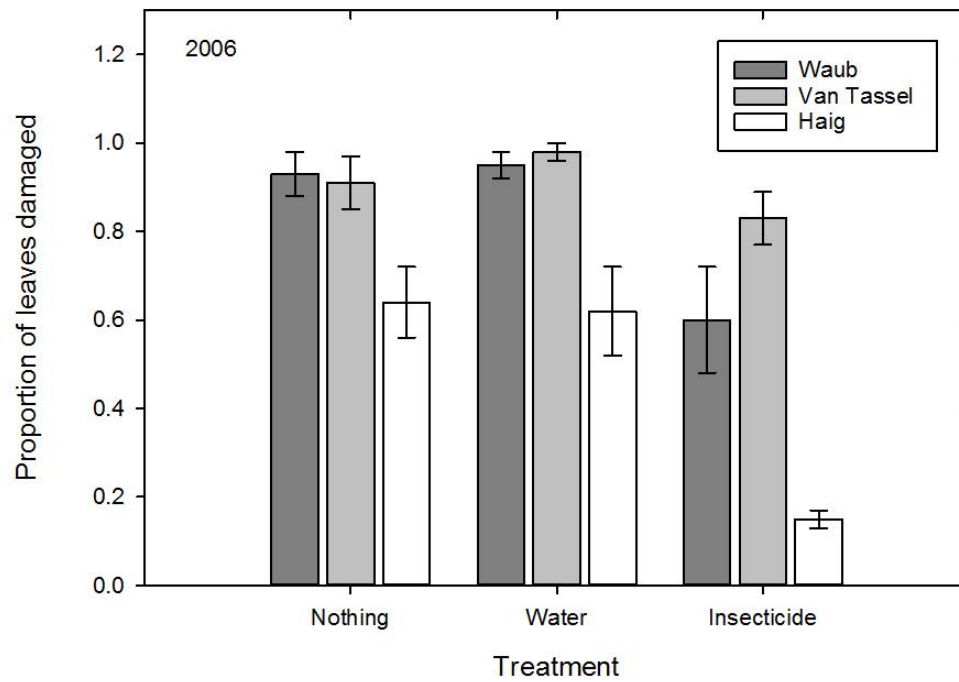
**Table 4**

Regression results and means for experimental *Desmanthus illinoensis* plant neighborhood. The dependent variable for the regressions was proportion of leaves damaged for the focal/ experimental *D. illinoensis* plant.

		R <sup>2</sup>	p	Mean (SE)
2006	Proportion Grass	<b>0.67</b>	<b>&lt;0.01</b>	55% (2)
	Species Richness	0.07	0.2	4.0 (0.2)
	Proportion Forb	0.05	0.2	10% (1)
	Proportion Legume	0.05	0.2	4% (2)
	Grass Richness	0.05	0.3	3.2 (0.1)
2007	Proportion Grass	<b>0.39</b>	<b>&lt;0.01</b>	60% (2)
	Species Richness	0.14	0.08	3.8 (0.2)
	Proportion Forb	0.11	0.13	8% (1)
	Proportion Legume	0.3	0.4	2% (1)
	Grass Richness	0.13	0.1	3.0 (0.1)
2008	Proportion Grass	<b>0.46</b>	<b>&lt;0.01</b>	70% (1)
	Species Richness	0.03	0.42	3.2 (0.2)
	Proportion Forb	0.08	0.2	5% (1)
	Proportion Legume	0.02	0.5	3% (2)
	Grass Richness	0.01	0.72	2.6 (0.1)

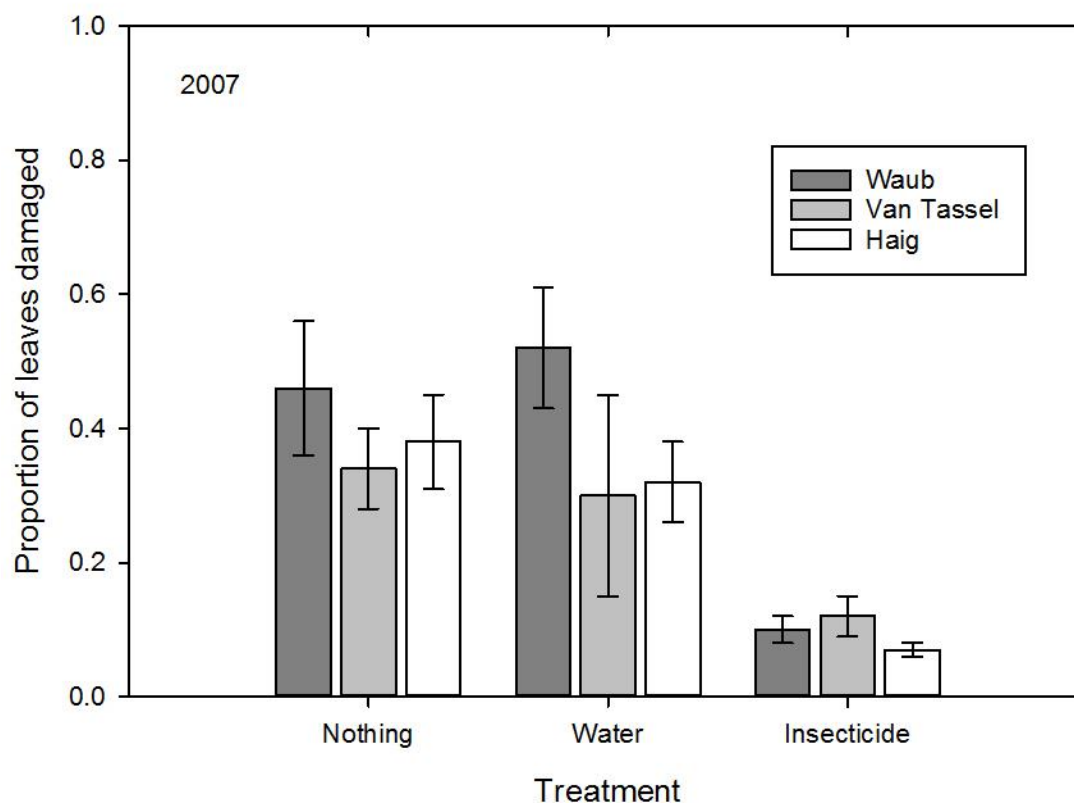
**Table 5**Species found in the neighborhoods of experimental *Desmanthus illinoensis* plants

Species	Type	Waub	Haig	VanTassel
<i>Artemesia ludoviciana</i>	Forb	X		
<i>Asclepias syriaca</i>	Forb		X	
<i>Asclepias verticillata</i>	Forb		X	
<i>Aster ericoides</i>	Forb	X	X	
<i>Conyza canadensis</i>	Forb			X
<i>Kuhnia eupatorioides</i>	Forb	X	X	
<i>Oxalis stricta</i>	Forb	X	X	X
<i>Plantago sp.</i>	Forb			X
<i>Rosa arkansana</i>	Forb	X	X	
<i>Vernonia baldwinii</i>	Forb		X	
<i>Viola sp.</i>	Forb			X
<i>Andropogon gerardi</i>	Grass	X		
<i>Bouteloua curtipendula</i>	Grass	X	X	
<i>Bromus tectorum</i>	Grass			X
<i>Panicum virgatum</i>	Grass	X		
<i>Poa pratensis</i>	Grass		X	X
<i>Schizachrium scoparium</i>	Grass	X	X	
<i>Sorghastrum nutans</i>	Grass	X		
<i>Stipa spartea</i>	Grass		X	
<i>Desmanthus illinoensis</i>	Legume	X	X	X



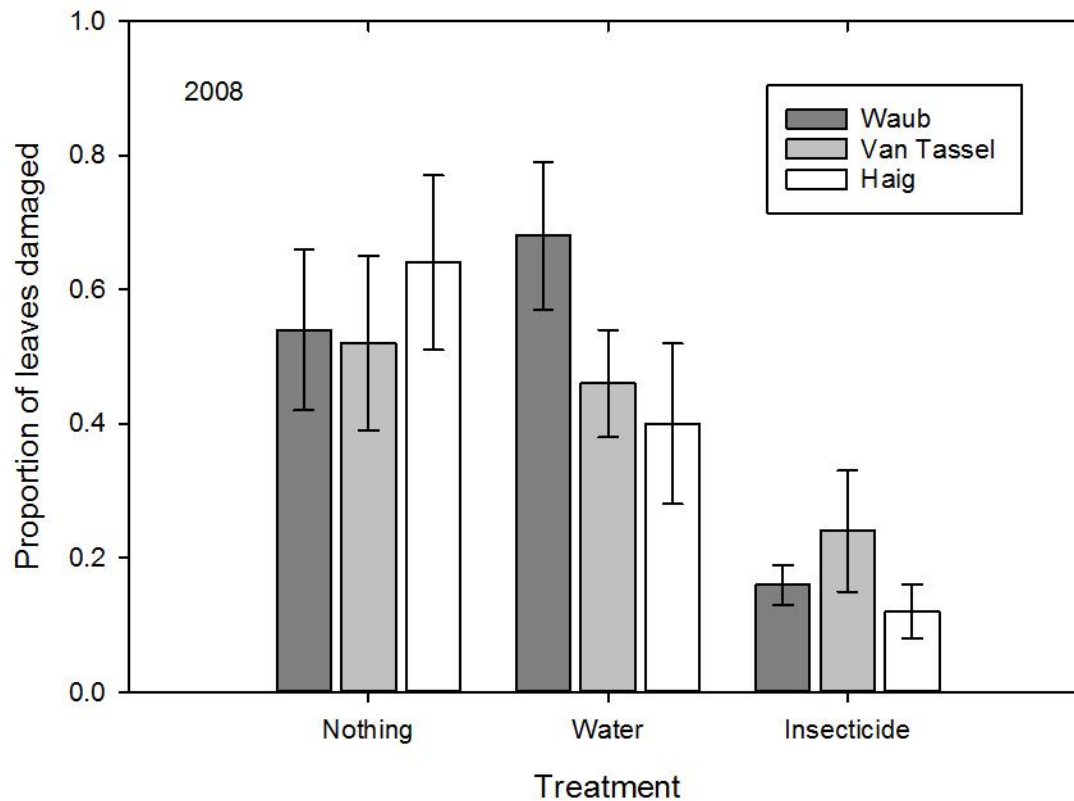
**Figure 1**

In 2006, the proportion of leaves damaged on *Desmanthus illinoensis* plants was significantly reduced with herbivore exclusion (insecticide:  $F_{2,4} = 15.80$ ,  $P = 0.01$ ; site:  $F_{2,4} = 28.79$ ,  $P = 0.004$ ). Each bar represents the mean of nine plants.



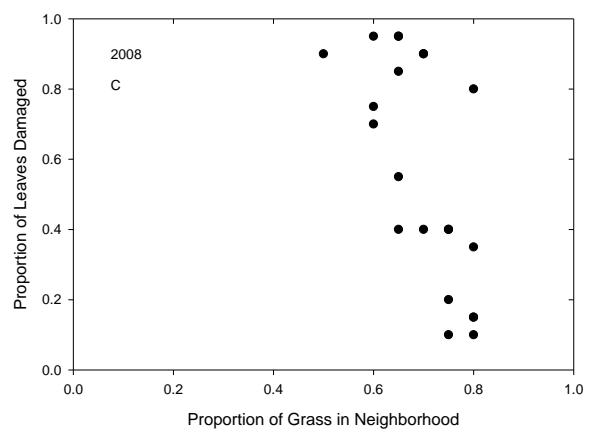
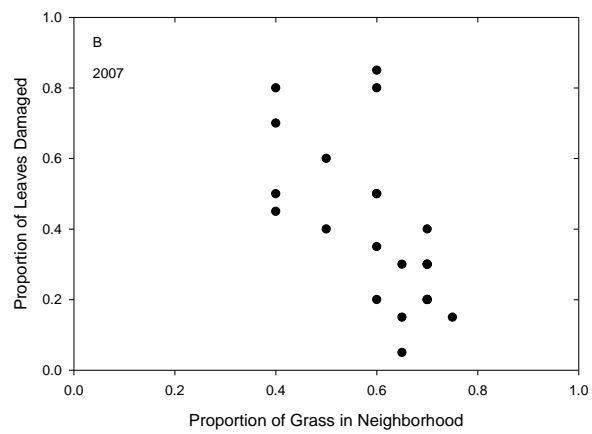
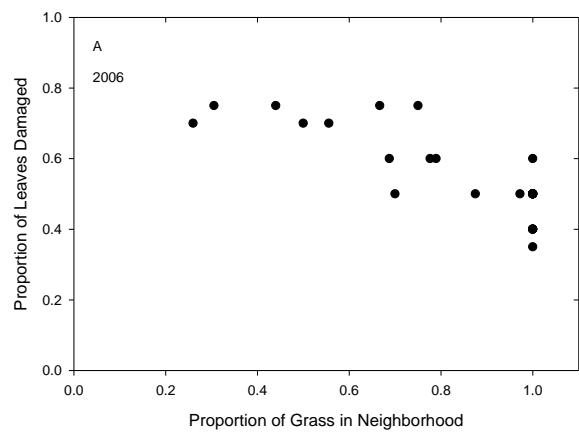
**Figure 2**

In 2007, the proportion of leaves damaged on *Desmanthus illinoensis* plants was significantly reduced with herbivore exclusion ( $F_{2,4} = 15.83$ ,  $P = 0.01$ ; site and interaction  $P > 0.2$ ). Not all plants in the experiment re-emerged in 2007. For the untreated control, each bar is the mean of 8 plants in Waub Prairie, 6 plants in Van Tassel Pasture, and 9 plants in Haig Prairie. For the water only control, each bar is the mean of 9 plants in Waub Prairie, 5 plants in Van Tassel Pasture, and 7 plants in Haig Prairie. For the insecticide treatment, each bar is the mean of 9 plants in Waub Prairie, 7 plants in Van Tassel Pasture, and 9 plants in Haig Prairie.



**Figure 3**

In 2008 the proportion of leaves damaged on *Desmanthus illinoensis* plants was significantly reduced with herbivore exclosure ( $F_{2,4} = 11.2$ ,  $P = 0.02$ ; site and interaction  $P > 0.3$ ). Not all plants in the experiment re-emerged in 2008. For the untreated control, each bar is the mean of 8 plants in Waub Prairie, 7 plants in Van Tassel Pasture, and 6 plants in Haig Prairie. For the water only control, each bar is the mean of 9 plants in Waub Prairie, 7 plants in Van Tassel Pasture, and 5 plants in Haig Prairie. For the insecticide treatment, each bar is the mean of 7 plants in Waub Prairie, 4 plants in Van Tassel Pasture, and 7 plants in Haig Prairie.



**Figure 4**

There was a significant relationship between the proportion of grass within the neighborhood of experimental plants and the proportion of leaves damaged. With greater grass cover there were proportionally fewer leaves damaged for 2006 (A), 2007 (B), and 2008 (C).

**Title: ROW SPACING AND SEEDING DENSITY AFFECTS YIELD IN A PERENNIAL LEGUME  
(*DESMANTHUS ILLINOENSIS*) / GRASS (*THINOPYRUM INTERMEDIUM*) BICULTURE**

**Abstract**

Crop intensification is characterized by utilizing more land and inputs, less crop diversity, and greater crop density. In contrast, perennial cropping systems use native prairie as a model and in addition to perenniality, perennial cropping systems model diverse prairie communities with polyculture. Possible benefits of perennial polyculture include increased yield with lower resource inputs. Perennial cropping systems also allow for more complex planting arrangements (e.g. crop frequency, intercrops, and row spacings) that could confer specialist insect pest resistance via reduced host plant apparency, changes in herbivore attraction, and host plant tissue quality. Such insect resistance could also contribute to higher perennial crop yields. *Desmanthus illinoensis* (Illinois Bundleflower), a legume, and *Thinopyrum intermedium* (Wheatgrass), a grass, are in the early stages of domestication as perennial grain crops. Here, we assess yields and seed herbivory of these two species planted in two different row spacings and five different initial seeding densities. Biculture seed yield was very productive. Seed yield by *T. intermedium* was greatest when it was in biculture with *D. illinoensis*. Twice as much *T. intermedium* seed was produced, by mass, in the 33% *D. illinoensis* seeded treatment than when *T. intermedium* was in monoculture (0% *D. illinoensis* crop frequency treatment). The greatest seed production, by mass, was in *D. illinoensis* monoculture, but there was no significant effect of crop frequency or row spacing on *D. illinoensis* seed production. Land equivalent ratios of the bicultures indicate that it would take about twice as much land to grow the equivalent seed yield from monocultures. The land equivalent ratios in our bicultures ranged from 1.9 (SE 0.4) to 2.5 (SE 0.4). Row spacing and crop frequency had very little effect on vegetative biomass, seed herbivory or weeds in the polyculture for *T. intermedium* or *D. illinoensis*. There was a



marginally significant effect of crop frequency on herbivory for *T. intermedium*; there was less herbivory on *T. intermedium* for the 50% and 100% *D. illinoensis* crop frequency treatments. Results suggest that biculture can be a beneficial cropping strategy for these two perennial crop species, and that reduced intraspecific competition by niche partitioning rather than reduced yield loss to insect herbivores was the mechanism of increased seed yield in biculture.

## Introduction

Humanity's demands for food, fiber, and fuel derived from agricultural products are expected to increase while current agricultural practices that utilize annual crops are facing increasing challenges such as rising costs of fuel and fertilizer, land degradation, and changing climate (Glover 2010; Glover and Reganold 2010). Perennializing grain cropping systems has been proposed as a way to mitigate such challenges (e.g. Jackson 1980; Glover and Reganold 2010). Examples of some of the advantages conferred by perennials are topsoil maintenance, increases in soil carbon, reductions in water and nitrate loss, and less fertilizer and pesticide inputs (Glover and Reganold 2010; Glover 2010). Perennial cropping systems use native prairie as a model and in addition to perenniality, perennial cropping systems model diverse prairie communities with polyculture (Jackson 1980). Increased plant community diversity can result in greater productivity/yield (Vandermeer 1995; Tilman et al., 1996; Hector, 1998; Hooper et al. 2005; Cardinale et al. 2007; Fargione et al. 2007). The ecological benefits of intercropping have been hypothesized to be reduced competition (the competitive production principle) and facilitation (Vandermeer 1995). The competitive production principle results in greater productivity with increased crop diversity through different crop species occupying the same space and having different patterns of resource use (niche partitioning) (Vandermeer 1995). In the case of facilitation, one crop species is thought to benefit the other crop species (Vandermeer 1995). Facilitation could be through nitrogen inputs by nitrogen-fixing crop species (Cox et al. 2006). Another mechanism of facilitation among crop species could be associational defense against herbivores (Root 1973).

*Desmanthus illinoensis*, a nitrogen-fixing legume, and *Thinopyrum intermedium*, a grass, are in the early stages of domestication as perennial grain crops (DeHaan et al. 2005, Cox et al. 2006,

Glover et al. 2007). In polyculture, the presence of *D. illinoensis* has been found to increase yield (above-ground biomass or seed production) of some neighboring grass species (Dovel et al. 1990, Piper 1993, Posler et al. 1993, Springer et al. 2001). However, legume density and polyculture design can influence whether nitrogen fixation by legumes can supply sufficient nitrogen to perennial polycultures (Crews 2005).

The influence of legume density and polyculture design may also affect insect herbivore management in agroecosystems. For example, by affecting the neighborhood composition of crop species, the composition of polycultures may have implications for insect herbivory on crop plants. In a process known as associational resistance or associational defense, some plants may experience less herbivory when co-occurring with heterospecific neighbors than in monoculture (Root 1973; Andow 1991). In contrast, some plant hosts may experience associational susceptibility, or more herbivory when in polyculture compared to monoculture (Root 1973; Andow 1991). Neighboring plants may affect insect herbivory through altered insect herbivore attraction or numerical responses of herbivores (Hamback and Beckerman 2003; Agrawal 2004). Furthermore, through changes in the resources available for plant growth, plant neighbors may affect tissue quality and availability, resistance traits, or compensatory abilities of target plant species (Machinski and Whitham 1989, Andow 1991, Hamback and Beckerman 2003, Agrawal 2004). Leguminous plants, which often have associations with nitrogen fixing bacteria, provide a clear example of such compositional effects on plant herbivory. A positive relationship was found between presence of legumes and herbivore abundance and a negative relationship between plant C:N and herbivore abundance (Haddad et al. 2001). In another experiment a relationship between legume presence and increases in numbers of herbivorous and predaceous insects was observed (Koricheva 2000). Moreover, herbivory on legumes may result in changes

in the amounts of nitrogen available to other plant species. For example, following defoliation of *Trifolium repens*, a legume, there was a five-fold increase in uptake of *T. repens*-derived nitrogen by a neighboring grass, *Lolium perenne* (Ayres et al. 2007). Alternatively, heavy defoliation by herbivores on legumes may result in decreased nitrogen fixation activity and thus decreased availability of nitrogen to plant neighbors (Johnson and Bentley 1991). In contrast, an experiment that manipulated insect herbivore exposure in multispecies mixtures found no effect of legume density or plant species richness on herbivore impact, although the presence of legumes was found to result in an increased size of the focal plant (Scherber et al. 2006). In sum, the presence of legumes may play a strong role in determining herbivore abundance and impact on a focal plant. Previous studies suggest that legumes may influence crop herbivory but less is known about legumes and crop herbivory in perennial cropping systems, and more specifically *Thinopyrum intermedium* – *Desmanthus illinoensis* bicultures.

Spatial arrangement (configuration) of host species may also affect insect herbivory. For example, spatial arrangement of host species can play an important role in chemical attraction of insect herbivores as they search for host plants (Stanton 1983). Spatial arrangement may have other critical effects such as altering plant apparency, distance among hosts, and intra- and interspecific competition (Weisser and Siemann 2004).

While little-studied in natural plant communities, the importance of spatial configuration has long been appreciated in agronomic contexts. For example, row spacing is a common agronomic practice that changes configuration and allows management of disease (Chang et al. 2007), weed competition (Vera et al. 2006; Wells et al. 2014), and available soil moisture (Dalley et al. 2006). Row spacing may also alter plant chemical resistance (Al-Tawaha and Seguin 2006). However,

less is known about the effect of row spacing on insect herbivory, particularly in perennial crop systems.

Here, we examine whether spatial configuration (row spacing) and crop frequency affected seed head herbivory and subsequent biomass and/or seed yield of a perennial polyculture of a legume, *D. illinoensis* (Illinois Bundleflower), and a grass, *T. intermedium* (Wheatgrass). Ultimately, perennial polycultures will need to be productive to be a viable option and initial seeding densities and row spacing could be useful tools in reducing losses to herbivores and optimizing biomass and seed yield.

## Methods

The experimental design was a five x two factorial design with five levels of *Desmanthus illinoensis* (Illinois Bundleflower) and *Thinopyrum intermedium* (Wheatgrass) crop frequency (0, 33, 50, 66, and 100% *D. illinoensis* seeded with remaining proportions of *T. intermedium*) and two row spacings (0.305 m; solid seeding and 0.914 m; row seeding) in a randomized complete block split design (eight replicate blocks). The whole plot factor was row spacing and the sub plot factor was crop frequency. The whole plots were seeded using a 1.82 m wide no till planter (three passes/ plot). The area of the sub plots was 5.5 m x 5.5 m and they were 5.5 m apart. For all treatments, the plots were seeded at a rate of 1,264 viable seeds/ m<sup>2</sup> in a replacement design. Viability rates for seed of both species were determined in the lab and the amount of seed to be planted was determined by mass. The experiment was in an experimental field at The Land Institute (38.82N, 97.62W; Saline County, Kansas, USA). The field was fallow for two years prior to the experiment and was located in a former floodplain.

For the 0.305 m (solid seeding) spacing treatment the seeds of one or both species (depending on proportions of *D. illinoensis* and *T. intermedium* seeded) were intermixed within 18 rows per plot. For the 0.914 m (row seeding) spacing, seeds of each species were planted separately in six rows. So, for example, the 66% *D. illinoensis* seeding treatment with 0.305 m row spacing had 18 rows with both species intermixed within rows at 66% *D. illinoensis* and 34% *T. intermedium*. In contrast, the 66% *D. illinoensis* seeding treatment with 0.914 m row spacing had two repeating patterns of two rows of *D. illinoensis* and one row of *T. intermedium* (six rows total).

The plots were planted on 29 April 2005 and were burned during March 2006 for weed control. Weeds were also managed in the 0.914 m row treatment by cultivation during July 2005 and May 2006. Emergence of both species occurred late in the first growing season (June 2005) and the plants remained small until the next growing season. After 2006, active management ceased.

In order to quantify biomass productivity, we harvested vegetation from 1 m<sup>2</sup> of an arbitrarily selected portion of the 5.5 m x 5.5 m plot. The samples were dried to constant mass, separated by species (*T. intermedium*, *D. illinoensis*, or weeds) and plant part (seeds or rest of the plant), and weighed in the lab. We analyzed plant biomass data by absolute mass and as a proportion. Absolute biomass allowed us to examine for effects of treatment on the productivity in each plot (e.g. seed yield, total plant biomass, and weed biomass). Proportional mass allowed us to examine whether the initial seeding frequencies were maintained within the plot. Measures of insect herbivory were made on inflorescences and differed slightly for each species. For each plot, one plant of each species was arbitrarily selected. For *T. intermedium*, we counted inflorescence spikes with undamaged seed and spikes where seed was removed or damaged by insect herbivores to calculate the proportion of spikes with damaged or removed seed. For *D. illinoensis*, we counted initiated but insect damaged seed heads (including aborted seed heads)

and matured seed heads to calculate the proportion of seed heads matured. Herbivory measures for both species occurred at harvest (August 2008). We calculated a land equivalent ratio (LER) to compare seed yields among plots that were intercropped, where  $LER = (\text{yield of intercropped IBF} / \text{yield of IBF in monoculture}) + (\text{yield of intercropped wheatgrass} / \text{yield of wheatgrass in monoculture})$  (Gliessman 1998). An LER greater than one indicates that an intercrop produces greater yield than a monoculture; an LER less than one indicates a monoculture produces greater yield than an intercrop. Analyses of variance and regressions were performed for each species using SPSS 21 (IBM 2013) for biomass and herbivory measures.

## Results

### *Wheatgrass*

Absolute *Thinopyrum intermedium* biomass differed significantly between the row spacing treatments but the initial proportion of seed planted did not significantly affect absolute biomass (Table 1). With wider row spacing there was greater *T. intermedium* biomass harvested (Figure 1). The proportion, by mass, of *T. intermedium* within the plots also significantly differed among the row spacings, and by the initial proportion of seed planted (Table 1). Proportionally, there was greater *T. intermedium* in the wider row spacing (Figure 2) and greater *T. intermedium* in the 0% *Desmanthus illinoensis* seed planted treatment (Figure 3). Among the 33%, 50%, and 66% *D. illinoensis* seed planted treatments the proportion of *T. intermedium* biomass did not differ much (Figure 3). The monocultures of *T. intermedium* had weeds. Therefore, the proportion of biomass of *T. intermedium* in monoculture was not 100% *T. intermedium* (Figure 3). Neither row spacing nor initial proportions of *D. illinoensis* seeded affected the number of *T. intermedium* spikes with herbivory (Table 1).

### ***Illinois Bundleflower***

Absolute *Desmanthus illinoensis* biomass did not differ significantly between row spacing treatments or by the initial proportion of seed planted (Table 2). The proportion of *D. illinoensis* harvested within the plots by mass did not differ significantly between row spacing treatments, but did differ significantly among the initial proportion of seed planted (Table 2). The greatest proportion of *D. illinoensis* harvested was in the 100% *D. illinoensis* seeded treatment; the least proportion of *D. illinoensis* harvested was in the least (33%) *D. illinoensis* seeded treatment (Figure 4). However, there was very little difference in the proportion of *D. illinoensis* harvested in the 50% and 66% seeded treatments (Figure 4). The proportion of *D. illinoensis* harvested when grown in monoculture (100% seeded treatment) was not 100% *D. illinoensis* because there were weeds (Figure 4). The proportion of seed heads matured did not differ significantly between row spacing treatments but was marginally significantly different among the seeding proportion treatments (Table 2). A greater proportion of seed heads, a measure of seed head herbivory, were matured when *D. illinoensis* was seeded at 50% and 100% (Figure 5).

### ***Weeds, seed yield, and LER***

Weed biomass and proportional weed biomass in the plots did not significantly differ between the row spacing treatments or among the crop frequency treatments (Table 3). Among the row spacing treatments, there were, on average, 41.8 g (SE 11.8) of weed biomass in the 0.914 m row spacing and 65.6 g (SE 15.7) of weed biomass in the 0.305 m row spacing. In the 0.914 m row spacing, weeds were 16% (SE 5) of all above-ground biomass while in the 0.305 m row spacing weeds were 26% (SE 6) of above-ground biomass. Among the seeding frequency treatments, weed biomass was least (proportionally and for absolute biomass) in the 50% *D. illinoensis* seeded treatment and the *D. illinoensis* monoculture (mean weed biomass: 0%: 61.6g, SE 25.6;



33%: 68.1g, SE 24.0; 50%: 40.7g, SE 17.4; 66%: 56.0g, SE 20.2; 100%: 42.2g, SE 19.8; and mean proportion weed biomass: 0%: 30.0%, SE 11.0; 33%: 24.4%, SE 8.1; 50%: 14.3%, SE 5.9; 66%: 22.9%, SE 9.0; 100%: 14.3%, SE 7.0). The dominant weed was *Sorghum halepense* for all of the experimental plots.

Seed yield for both *D. illinoensis* and *T. intermedium* was strongly and positively related to plant biomass (*D. illinoensis*:  $R^2 = 0.5$ ,  $P < 0.01$ ; *T. intermedium*:  $R^2 = 0.2$ ,  $P < 0.01$ ). Overall, the greatest seed production, by mass, was in *D. illinoensis* monoculture (Table 1), but there was no significant effect of crop frequency or row spacing on *D. illinoensis* seed production (Tables 2 and 4). *Thinopyrum intermedium* produced more seed, by mass, in polyculture and the greatest mass of seed produced occurred when this species was seeded with *D. illinoensis* at 33% and 50%, but there was not a statistically significant effect of crop frequency or row spacing on *T. intermedium* seed production (Tables 1 and 4). However, for total seed yield (*D. illinoensis* and *T. intermedium* combined) there was a significant effect of crop frequency ( $F_{4,7} = 13.2$ ,  $P = 0.002$ ) but not for row spacing (Tables 3 and 4). Seed yield was least in the *T. intermedium* monoculture and greatest in the *D. illinoensis* monoculture (Table 4). Among the crop frequency treatments where seeds of both crop species were planted, the greatest yield was in the 33% *D. illinoensis* seeded treatment (Table 4). The land equivalent ratio (LER) in the 33% *D. illinoensis* treatment (2.5, SE 0.4) was greater than in the 50% and 66% *D. illinoensis* treatments (50%: 2.4, SE 0.4; 66%: 1.9, SE 0.4; Table 4). For all three of the *D. illinoensis* seeding treatments that were bicultures, the LER was above 1.0 which indicates that the bicultures produced greater seed yield than the monocultures (i.e. the 0% and 100% *D. illinoensis* seeding treatments).

## Discussion

Overall, we found very little support for associational susceptibility or associational defense as an herbivory-reducing mechanism in our polycultures. Furthermore, row spacing also did not affect herbivory on our experimental crop species. In our experiment the predominant herbivores were grasshoppers (pers. observation), which are generalist herbivores (Joern 1979, Joern 1983). Thus, our treatments of seeding frequency and row spacing that were intended to vary host plant apparency and proximity were not effective for these generalist herbivores. However, our bicultures of *Desmanthus illinoensis* and *Thinopyrum intermedium* were productive, and more productive than our monocultures (Table 4).

There was no significant effect of crop frequency or configuration on absolute or proportional weed biomass in our experiment. This is somewhat surprising in that reduced row spacing often helps to suppress weeds (e.g. Berenstein et al. 2014; Wells et al. 2014). For example, in organic soybean cropping systems, reduced row spacing (e.g. 76 cm vs. 38 cm, Wells et al. 2014) results in increased weed suppression. In organic soybean systems, the soybean canopy closes much earlier in the growing season when rows are closer together. This prevents light from reaching recently emerged weeds; when rows are closer together, organic soybeans are better able to out compete weeds for light (Berenstein et al. 2014; Wells et al. 2014). Weed suppression in our experiment may have differed from that of the organic soybean cropping systems due to differing life history traits of the dominant weed(s). In the organic soybean cropping systems the dominant weeds regenerated annually from a persistent seed bank (Berenstein et al. 2014, Wells et al. 2014), while in the *D. illinoensis*- *T. intermedium* biculture the dominant weed, *Sorghum halepense*, is capable of clonal reproduction from rhizomes (Follak and Essl 2013). Clonal plant species can translocate assimilates from unshaded ramets to shaded ramets within the genet

(Hartnett and Bazzaz 1983, Hartnett and Bazzaz 1985). Thus, in our experiment, the dominant weed likely was less susceptible to light competition, making cover and canopy closure much less important, and this may explain the lack of an effect of row spacing on weed suppression. It should also be noted that in our experiment we stopped cultivating after one year. Depending on the weed species, continuing to cultivate for weed reduction could certainly result in more effective weed control. However, continued cultivation could only be implemented for the wide (0.914m) row spacing because equipment would not be able get in to cultivate the narrow (0.305m) row spacing. Given the rhizomatous nature of *S. halepense*, the dominant weed in our experiment, we do not expect that continuous cultivation would have been effective.

*Thinopyrum intermedium* produced more seed (Table 4) when it comprised less of the cover for the plot (Figures 2 and 3). The greatest mass of seed produced by *T. intermedium* was when it was in biculture with *D. illinoensis*. For example, twice as much *T. intermedium* seed was produced, by mass, in the 33% *D. illinoensis* seeded treatment than when *T. intermedium* was in monoculture (0% *D. illinoensis* seed treatment). Twice as much seed was produced in the 33% treatment even though actual *T. intermedium* cover was about half of that in the *T. intermedium* monoculture (Table 4 and Figure 3). Our observations of less *T. intermedium* cover with closer row spacing and greater initial seeding rates suggest that intraspecific competition for *T. intermedium* is high and intraspecific competition is greater than interspecific competition. We found a similar result for *D. illinoensis*. When *D. illinoensis* was seeded at the 33% *D. illinoensis* seeding frequency, *D. illinoensis* had the least amount cover among the seeding treatments except for when *T. intermedium* was in monoculture (Figure 4). However, seed yield relative to seed input and *D. illinoensis* cover was greatest for the 33% *D. illinoensis* seeding frequency (Figure 4). Our data therefore also suggest that intraspecific competition is greater

than interspecific competition for *D. illinoensis*. Greater intraspecific than interspecific competition is a signal of niche partitioning.

Likewise, our analysis of land equivalent ratios (Table 4) suggests that the *D. illinoensis*- *T. intermedium* bicultures were more productive than the monocultures of both crops. For all three bicultures, the land equivalent ratios indicate that it would take about twice as much land to grow the equivalent seed yield from monocultures. The land equivalent ratios in our bicultures ranged from 1.9 (SE 0.4) to 2.5 (SE 0.4; Table 4). In a recent meta-analysis of legume-grass intercrops, most of the reported land equivalent ratios were between 1.0 and 1.5 (Pelzer et al. 2014). Land equivalent ratios over 2.0 were also reported, although much less frequently than those between 1.0 and 1.5 (Pelzer et al. 2014).

In the *D. illinoensis*- *T. intermedium* bicultures we observed overyielding. We attribute the observed overyielding to reduced competition (niche partitioning), but facilitation, perhaps in part through nitrogen-fixation, could have also contributed. Facilitation and reduced competition have been observed to be the mechanisms underlying overyielding in other legume-grass intercrops (Vandermeer 1995; DeHaan et al. 2010; Pelzer et al. 2014). In our experiment, biological fixation of nitrogen by *D. illinoensis* may have resulted in greater amounts of soil nitrogen available to *T. intermedium*.

Our observations of competitive interactions, yield, and response to row spacing of *D. illinoensis*, a legume, and *T. intermedium*, a grass, are inconsistent with a recent meta-analysis of co-planted legumes and cereals (Ren et al. 2014). The meta-analysis suggests that legume-cereal polyculture tends to only benefit the cereal and the cereal also tends to respond more to row and mixed intercropping (Ren et al. 2014). In our polyculture, *T. intermedium* produced greater

absolute biomass with greater row spacing while there was no difference in *D. illinoensis* absolute biomass among the row spacing treatments. However, in contrast to the meta-analysis both *T. intermedium* and *D. illinoensis* produced greater seed yield in polyculture than in monoculture.

Another examination of *D. illinoensis* seed yield observed 147 g/ m<sup>2</sup> of seed produced (Piper 1993). We found much less than that in our experiment. The most seed produced in our plots was 7.5 g/ m<sup>2</sup> of *D. illinoensis* seed produced in *D. illinoensis* monoculture. The reasons for the dramatic difference in *D. illinoensis* yield are not clear but a possible reason could be weed infestation. We had an aggressive weed, *S. halepense*, in our experiment and it could have reduced yield.

There are at least two future directions of research suggested by our experiment. In our experimental field we had widespread infestation of *S. halepense* and high densities of grasshoppers, a generalist herbivore. Specialist herbivore search and/or feeding behavior is expected to be affected by the presence of heterospecifics (associational defense, Root 1973). However, generalist herbivores, such as grasshoppers, are not expected to be affected by host plant diversity or configuration. It would be useful to investigate weed suppression and insect herbivory under different weed and insect pest conditions. Furthermore, our results could be different in a subsequent year. For example, in another examination of productivity and diversity, productivity increased with time (Fargione et al. 2007). Another future direction of research could be to examine the mechanisms underlying the observed overyielding of *D. illinoensis* and *T. intermedium* (Table 4). Investigation of the roles of biological nitrogen fixation, intraspecific competition, and their interaction would provide greater insights into our observation of overyielding.

### ***Implications for perennial polyculture***

Row spacing could be important in perennial polycultures with *T. intermedium*. We found more *T. intermedium* biomass with wider rows; wider rows could provide another benefit in that they can be cultivated for weed control years after planting. Finally, our bicultures were productive which suggests that incorporating crop diversity could benefit perennial polyculture.

## Literature Cited

- Agrawal, A.A. 2004. Resistance and Susceptibility of Milkweed: Competition, Root Herbivory, and Plant Genetic Variation. *Ecology*. 85: 2118-2133.
- Al-Tawaha, A.M. and P. Seguin. 2006. Seeding date, row spacing, and weed effects on soybean isoflavone concentrations and other seed characteristics. *Canadian Journal of Plant Science*. 86: 1079-1087.
- Andow, D.A. 1991. Vegetational diversity and arthropod population response. *Annual Review of Entomology*. 36: 561-586.
- Ayres, E., K.M. Dromph, R. Cook, N. Ostle, and R.D. Bardgett. 2007. The influence of below-ground herbivory and defoliation of a legume on nitrogen transfer to neighboring plants. *Functional Ecology*. 21: 256-263.
- Bernstein, E.R., D. E. Posner, J.L., et al. 2014. Weed Community Dynamics and Suppression in Tilled and No-Tillage Transitional Organic Winter Rye-Soybean Systems. *Weed Science*. 62(1): 125-137.
- Cardinale, B.J., J.P. Wright, M.W. Cadotte, I.T. Carroll, A. Hector, D.S. Srivastava, M. Loreau, and J.J. Weis. 2007. Impacts of plant diversity on biomass production increase through time because of species complementarity. *PNAS*. 104: 18123-18128.
- Chang, K.F., H.U. Ahmed, S.F. Hwang, B.D. Gossen, R.J. Howard, T.D. Warkentin, S.E. Strelkov, and S.F. Blade. 2007. Impact of cultivar, row spacing and seeding rate on ascochyta blight severity and yield of chickpea. *Canadian Journal of Plant Science*. 87: 395-403.
- Cox, T.S., J.D. Glover, D.L. Van Tassel, C.M. Cox, L.R. DeHaan. 2006. Prospects for Developing Perennial Grain Crops. *BioScience*. 56(8): 649-659.
- Crews, T. E. 2005. Perennial crops and endogenous nutrient supplies. *Renewable Agriculture and Food Systems*. 20: 25-37.
- Dalley, C.D., M.L. Bernards, and J.J. Kells. 2006. Effect of Weed Removal Timing and Row Spacing on Soil Moisture in Corn (*Zea mays*). *Weed Technology*. 20: 399-409.
- DeHaan, L.R., D.L. Van Tassel, T.S. Cox. 2005. Perennial grain crops: A synthesis of ecology and plant breeding. *Renewable Agriculture and Food Systems*. 20: 5-14.
- DeHaan, L.R., S. Weisberg, D. Tilman, D. Fornara. 2010. Agricultural and biofuel implications of a species diversity experiment with native perennial grassland plants. *Agriculture, Ecosystems and Environment*. 137: 33-38.
- Dovel, R.L., M.A. Hussey, and E.C. Holt. 1990. Establishment and survival of Illinois bundleflower interseeded into and established Kleingrass pasture. *Journal of Range Management*. 53: 153-156.
- Fargione, J., D. Tilman, R. Dybzinski, J.H.R. Lambers, C. Clark, W.S. Harpole, J.M.H. Knops, P.B. Reich, M. Loreau. 2007. From Selection to complementarity: shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. *Proc. R. Soc. B*. 274: 871-876.

- Follak, S. and F. Essl. 2013. Spread dynamics and agricultural impact of *Sorghum halepense*, an emerging invasive species in Central Europe. *Weed Research*. 53 (1): 53-60.
- Gliessman, S. 1998. *Agroecology: Ecological Processes in Sustainable Agriculture*. Sleeping Bear Press, Chelsea, MI.
- Glover, J.D. 2010. Harvested perennial grasslands: Ecological models for farming's perennial future. *Agriculture, Ecosystems, and Environment*. 137: 1-2.
- Glover, J. and J. Reganold. 2010. Perennial Grains: Food Security for the Future. *Issues in Science and Technology*. 26.2: 41-47.
- Glover, J.D., C.M. Cox, and J.P. Reganold. 2007. Future Farming: A Return to Roots? *Scientific American*. p. 82-89.
- Haddad, N.M., D. Tilman, J. Haarstad, M.E. Ritchie, and J.M.H. Knops. 2001. Contrasting effects of plant richness and composition on insect communities: a field experiment. *American Naturalist*. 158: 17-35.
- Hamback, P.A. and A.P. Beckerman. 2003. Herbivory and plant resource competition: a review of two interacting interactions. *Oikos*. 101: 26-37.
- Hartnett, D. and F. Bazzaz. 1983. Physiological integration among intracolonial ramets in *Solidago canadensis*. *Ecology*. 64(4): 779-788.
- Hartnett, D. and F. Bazzaz. 1985. The integration of neighbourhood effects by clonal genets of *Solidago canadensis*. *Journal of Ecology*. 73: 415-428.
- Hector, A. 1998. The effects of diversity on productivity: detecting the role of species complementarity. *Oikos*. 82: 597-599.
- Hooper, D.U., F.S. Chapin III, J.J. Ewel, A. Hector, P. Inchausti, S. Lavorel, J.J. Lawton, D.M. Lodge, M. Loreau, S. Naeem, B. Schmid, H. Setälä, A.J. Symstad, J. Vandermeer, D. A. Wardle. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs*. 75: 3-35.
- IBM Corp. Released 2013. *IBM SPSS Statistics for Windows, Version 22.0*. Armonk, NY: IBM Corp.
- Jackson, W. 1980. *New Roots for Agriculture*. University of Nebraska Press. Lincoln, Nebraska.
- Joern, A. 1979. Feeding Patterns in Grasshoppers (Orthoptera: Acrididae): Factors Influencing Diet Specialization. *Oecologia*. 38: 325-347.
- Joern, A. 1983. Host Plant Utilization by Grasshoppers (Orthoptera: acrididae) from a Sandhills Prairie. *Journal of Range Management*. 36 (6): 793-797.
- Johnson, N.D. and B.L. Bentley. 1991. Symbiotic N<sub>2</sub>-fixation and the elements of plant resistance to herbivores: lupine alkaloids and tolerance to defoliation. Pp 45-63 In P. Barbosa, V.A. Krischik, C.G. Jones eds *Microbial Mediation of Plant-Herbivore Interactions*. John Wiley and Sons, New York.
- Koricheva, J., C.P.H. Mulder, B. Schmid, J. Joshi, and K. Huss-Danell. 2000. Numerical responses of different trophic groups of invertebrates to manipulation of plant diversity in grassland. *Oecologia*. 125: 271-282.



- Machinski, J. and T. G. Whitham. 1989. The continuum of plant responses to herbivory: the influence of plant association, nutrient availability, and timing. *American Naturalist*. 134 (1): 1-19.
- Pelzer, E., N. Hombert, M. Jeuffroy, and D. Makowski. 2014. Meta-Analysis of the effect of Nitrogen Fertilization on Annual Cereal-Legume Intercrop Production. 2014. *Agronomy Journal*. 106 (5): 1775-1786.
- Piper, J.K. 1993. Neighborhood effects on growth, seed yield, and weed biomass for three perennial grains in polyculture. *Journal of Sustainable Agriculture*. 4: 11-31.
- Posler, G.L., A.W. Lenssen, and G.L. Fine. 1993. Forage yield, quality, compatibility, and persistence of warm-season grass-legume mixtures. *Agronomy Journal*. 85: 554-560.
- Root, R.B. 1973. Organization of plant-arthropod association in simple and diverse habitats: the fauna of collards (*Brassica oleracea*). *Ecological Monographs*. 43: 95-124.
- Scherber, C., A. Milcu, S. Partsch, S. Scheu, and W.W. Weisser. 2006. The effects of plant diversity and insect herbivory on performance of individual plant species in experimental grassland. *Journal of Ecology*. 94: 922-931.
- Springer, T.L., G.E. Aiken, and R.W. McNew. 2001. Combining ability of binary mixtures of native, warm-season grasses and legumes. *Crop Science*. 41: 818-823.
- Stanton, M.L. 1983. *Spatial Patterns in the Plant Community and Their Effects upon Insect Search in Herbivorous Insects*. Academic Press. New York.
- Tilman, D. Wedin, D., J. Knops. 1996. Productivity and sustainability influenced by biodiversity in grassland ecosystem. *Nature*. 379: 3.
- Vandermeer, J. 1995. The Ecological Basis of Alternative Agriculture. *Annual Review of Ecology and Systematics*. 26: 201-224.
- Vera, C.L., S.M. Woods, and J.P. Raney. 2006. Seeding rate and row spacing effect on weed competition, yield, and quality of hemp in the Parkland region Saskatchewan. *Canadian Journal of Plant Science*. 86: 911-915.
- Weisser, W.W. and E. Siemann. 2004. The various effects of insects on ecosystem functioning *in Insects and Ecosystem Function*. Springer-Verlag. Berlin.
- Wells, M.S., S.C. Reberg-Horton, S.B. Mirsky. 2014. Cultural Strategies for Managing Weeds and Soil Moisture in Cover Crop Based No-Till Soybean Production. 2014. *Weed Science*. 62(3): 501-511.

**Table 1**

Analysis of variance results for wheatgrass (*Thinopyrum intermedium*).

		Absolute Biomass	Proportion Biomass	Number of Spikes with Herbivory	Seed Yield
Row Spacing	df	<b>1, 10</b>	<b>1, 10</b>	1, 10	1, 10
	F	<b>4.3</b>	<b>4.4</b>	0.1	0.53
	P	<b>0.06</b>	<b>0.06</b>	0.76	0.49
Crop Frequency	df	3, 8	<b>3, 8</b>	3, 8	3, 8
	F	0.6	<b>6.4</b>	0.11	3.45
	P	0.63	<b>0.02</b>	0.96	0.07
Row Spacing x Crop Frequency	df	3, 8	3, 8	3, 8	3, 8
	F	0.45	0.29	1.2	0.51
	P	0.99	0.83	0.37	0.73

**Table 2**Analysis of variance results for Illinois Bundleflower (*Desmanthus illinoensis*).

		Absolute Biomass	Proportion Biomass	Proportion Seed Heads Matured	Seed Yield
Row Spacing	df	1, 10	1, 10	1, 10	1, 10
	F	0.081	3.05	0.33	0.63
	P	0.78	0.11	0.58	0.45
Crop Frequency	df	3, 8	<b>3, 8</b>	<b>3, 8</b>	<b>3, 8</b>
	F	2.82	<b>11.8</b>	<b>3.6</b>	<b>15.01</b>
	P	0.11	<b>&lt;0.01</b>	<b>0.06</b>	<b>&lt; 0.01</b>
Row Spacing x Crop Frequency	df	3, 8	3, 8	3, 8	3, 8
	F	1.99	0.7	2.45	2.24
	P	0.19	0.58	0.14	0.17

**Table 3**

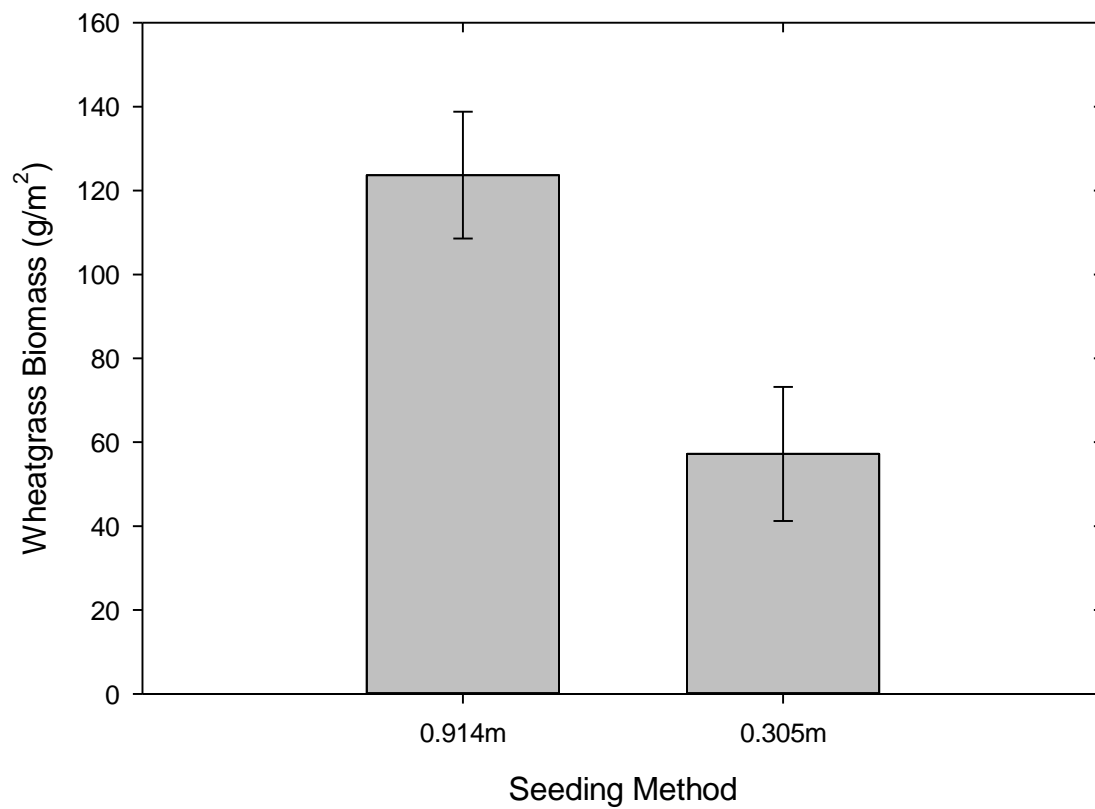
Analysis of variance results for weeds and combined seed yield of Illinois Bundleflower (*Desmanthus illinoensis*) and wheatgrass (*Thinopyrum intermedium*) biculture.

		Total Seed Yield	Absolute Weed Biomass	Proportional Weed Biomass
Row Spacing	df	1, 10	1, 10	1, 10
	F	0.93	0.73	0.06
	P	0.36	0.41	0.82
Crop Frequency	df	<b>4, 7</b>	4, 7	4, 7
	F	<b>13.15</b>	0.17	0.43
	P	<b>&lt;0 .01</b>	0.95	0.74
Row Spacing x Crop Frequency	df	4, 7	4, 7	4, 7
	F	1.64	0.75	1.14
	P	0.27	0.59	0.39

**Table 4**

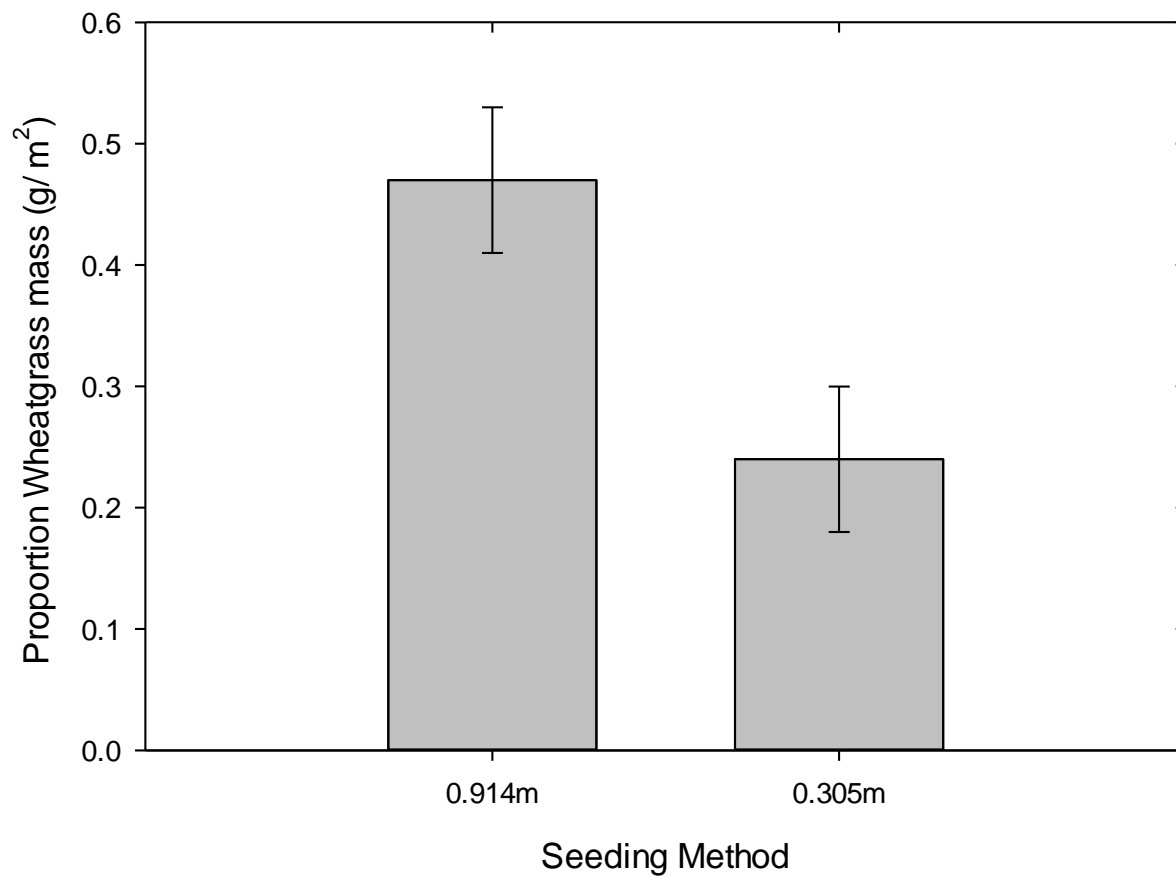
Mean seed harvested ( $\text{g/m}^2$ ) for both species among initial seeding treatments of *Desmanthus illinoensis*. Means and standard errors are reported ( $n=12$ ). *Thinopyrum intermedium* produced more seed, by mass, in polyculture while *Desmanthus illinoensis* produced more seed in monoculture. Calculation of the land equivalent ratio (LER) is a ratio that indicates how much land would be required to produce both crops in biculture in comparison to how much land would be required to grow each crop in monoculture (equation:  $\text{LER} = (\text{yield of intercropped IBF} / \text{yield of IBF in monoculture}) + (\text{yield of intercropped wheatgrass} / \text{yield of wheatgrass in monoculture})$ ). The LER is useful because allows one to compare productivity among intercrops. An LER greater than one indicates that intercropping is advantageous. For example, an LER of 2.0 would indicate that it would take twice as much land to produce two crops in monoculture than in biculture.

	0%	33%	50%	66%	100%
<i>Thinopyrum intermedium</i>	0.88 (0.2)	1.75 (0.4)	1.67 (0.5)	1.25 (0.4)	0
<i>Desmanthus illinoensis</i>	0	3.75 (1.0)	3.50 (0.5)	2.92 (0.7)	7.5 (2.1)
Total Seed ( $\text{g/m}^2$ )	0.88 (0.2)	5.50 (1.3)	5.17 (0.6)	4.17 (0.9)	7.5 (2.1)
Total Seed (kg/ha)	8.8 (2)	55.0 (13)	51.7 (6)	41.7 (9)	75 (21)
Land equivalent ratio	-	2.5 (0.4)	2.4 (0.4)	1.9 (0.4)	-



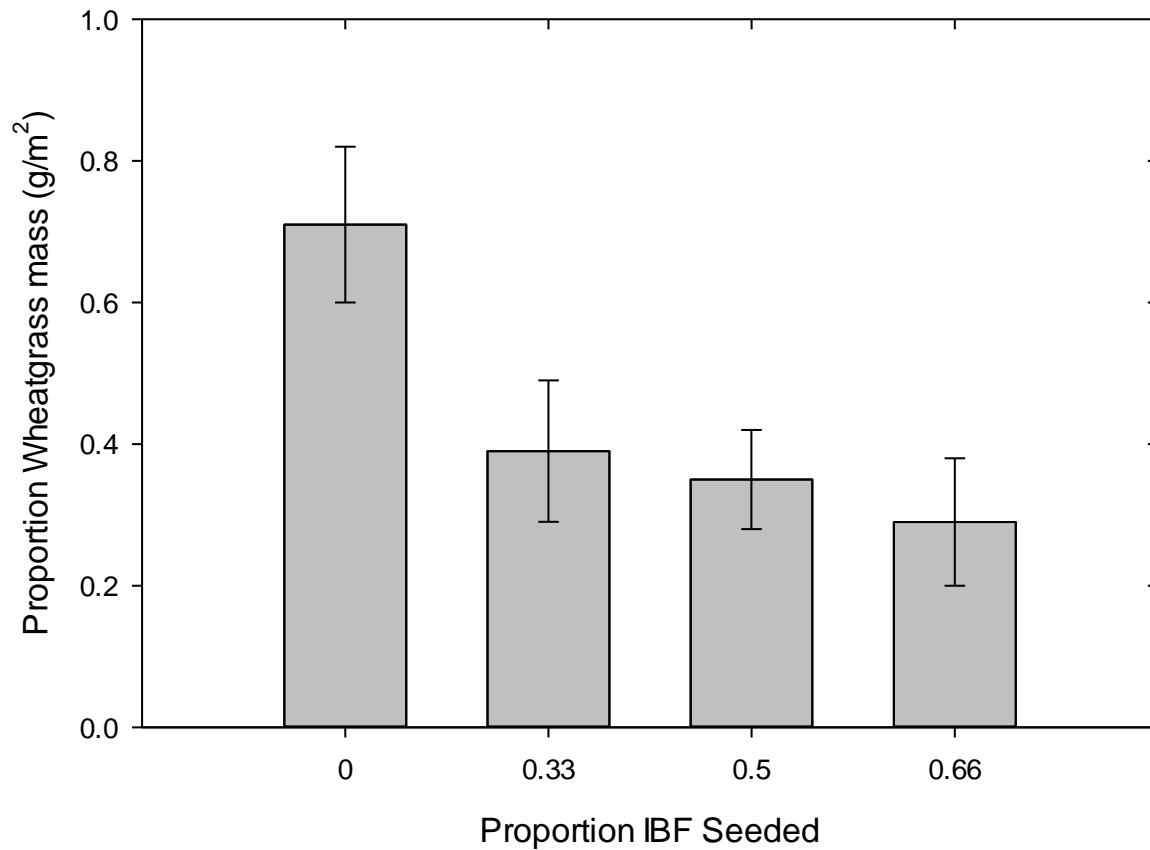
**Figure 1**

Wheatgrass (*Thinopyrum intermedium*) biomass harvested (g/m<sup>2</sup>) among the two row spacings. Bars represent 30 plots and error bars represent standard error. With greater row spacing there was greater wheatgrass biomass harvested.



**Figure 2**

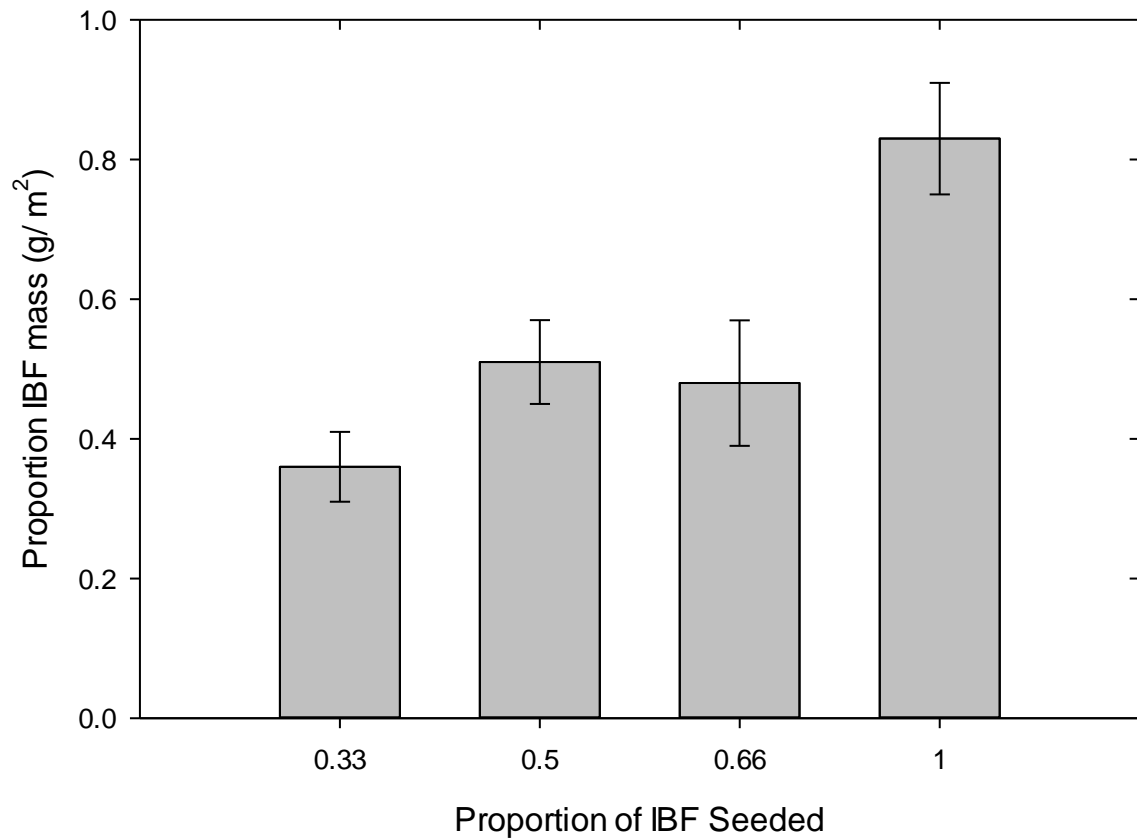
Proportion of wheatgrass (*Thinopyrum intermedium*) biomass harvested (g/m<sup>2</sup>) among the two row spacings. Bars represent 30 plots and error bars represent standard error. With greater row spacing there was proportionally greater wheatgrass biomass harvested.



**Figure 3**

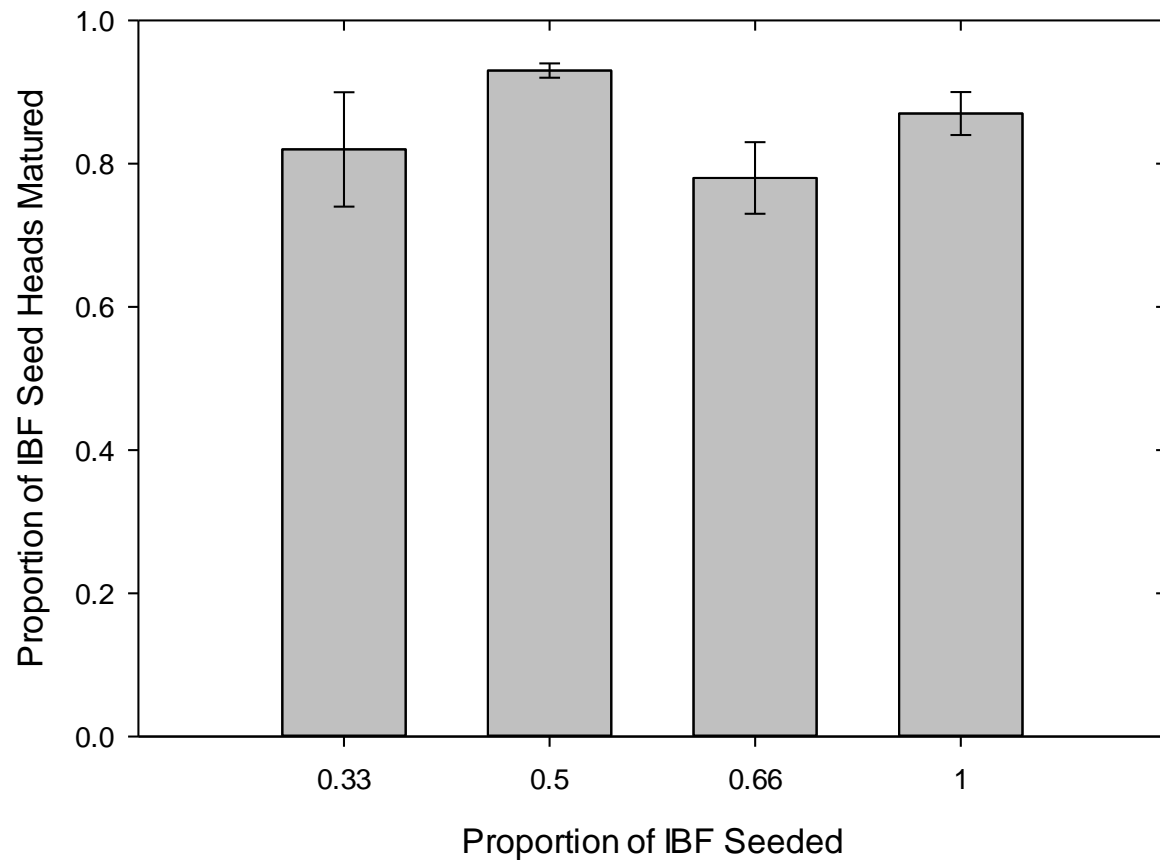
Proportion of wheatgrass (*Thinopyrum intermedium*) biomass harvested (g/m<sup>2</sup>) among the initial seeding treatments. The initial seeding treatments are expressed in the frequency of *Desmanthus illinoensis* (IBF, Illinois Bundleflower) seeded. Bars represent 12 plots and error bars represent standard error. The greatest proportions of wheatgrass harvested occurred in the 0% IBF, 100% wheatgrass seeded treatment. Otherwise, the initial proportion of seed did not affect later wheatgrass cover.





**Figure 4**

Proportion of Illinois Bundleflower (IBF; *Desmanthus illinoensis*) biomass harvested (g/m<sup>2</sup>) among the initial seeding treatments. Bars represent 12 plots and error bars represent standard error. The greatest proportion of Illinois Bundleflower was found when plots were seeded with 100% Illinois Bundleflower.



**Figure 5**

Proportion of Illinois Bundleflower (IBF; *Desmanthus illinoensis*) seed heads matured among treatments of initial proportion of Illinois Bundleflower seeded. Bars represent 12 plots and error bars represent standard error. Greater seed head maturation can be an indicator of less insect herbivory. Greater seed head maturation was observed in plots where 50% and 100% of *D. illinoensis* was seeded.

## Curriculum Vitae

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### EDUCATION:

- 2004- Present      Indiana University (Bloomington, IN): Ph.D., Ecology, Evolution, and Behavior (Biology), Minor: Plant Sciences  
*Dissertation:* Effects of Local Plant Neighborhood on Plant Herbivory in Perennial Polyculture Cropping Systems.
- 2000- 2003      University of Nebraska- Lincoln: M.S., Biological Sciences.  
*Thesis:* Native Insect Herbivory Provides Resistance to Invasive Spread by an Exotic Thistle.
- 1996-2000      Bucknell University (Lewisburg, PA): B.S., Major: Environmental Studies, Minor: Economics; Completed University Scholars Program.  
*Thesis:* Mycorrhizae influence the differential performance of two goldenrods across a soil-moisture gradient.

### PUBLICATIONS:

#### PEER REVIEWED PUBLICATIONS

- Glover, J.D., **Culman, S.W.**, DuPont, S.T., Broussard, W., **Young, L.**, Mangan, M., Mai, J., Crews, T.E., DeHaan, L.R., Buckley, D.H., Ferris, H., Reynolds, H., Turner, E., Wyse, D. 2010. Perennial grassland provides ecological benchmarks for agricultural sustainability. *Agriculture, Ecosystems and Environment* 137, p. 3-12. Stable URL: <http://dx.doi.org/10.1016/j.agee.2009.11.001>
- Louda, S., A. Parkhurst, K. Bradley, E. Bakker, J. Knops, E. Damschen, and **L. Young**. 2004. Spatial heterogeneity, not visitation, dominates variation in herbivory: reply. *Ecology* 85, p. 2906-2910. Stable URL: <http://www.jstor.org/stable/3450450>
- Bradley, K.L., E. Damschen, **L.M. Young**, D. Kuefler, S. Went, G. Wray, N.M. Haddad, J.M.H. Knops, and S.M. Louda. 2003. Spatial heterogeneity, not visitation, dominates variation in herbivory. *Ecology* 84, p. 2214-2221. Stable URL: <http://www.jstor.org/stable/3450045>

### CONTRIBUTED PRESENTATIONS

#### PRESENTATIONS

- Young, L.**, H. Reynolds, and L. DeHaan. 2009. Effects of prairie and agricultural plant neighborhoods on insect herbivory of a perennial legume. Ecological Society of America annual meeting, Albuquerque, NM.

#### SYMPOSIUM ORGANIZED

- From genes to watersheds: developing a post-contemporary agriculture (1888- 2058). 2009. co-organizers: J. Glover, **L. Young**, and H. Reynolds. Ecological Society of America Annual Meeting, Albuquerque, NM.

## POSTER PRESENTATIONS

- Young, L.,** M. Barbercheck, S. Mirsky, D. Weber. 2013. Wireworm populations increase dramatically in an organic reduced-tillage grain rotation in Maryland. Entomological Society of America Annual Meeting, Austin, TX.
- Young, L. M. S.** Tianna DuPont, J. Glover. 2008. Grasslands as benchmarks for agricultural sustainability: nematode and insect communities. Ecological Society of America Annual Meeting, Milwaukee, WI.
- Young, L.,** S. Louda. 2005. Native insect herbivory provides resistance to a thistle invasion. Ecological Society of America, Montreal, Quebec.
- Young, L.,** S. Louda. 2003. Differences in survival, traits, and herbivory of seedlings from native and invasive congeners. Ecological Society of America Annual Meeting, Savannah, GA.
- Young, L.,** S. Louda, 2002. Influence by native thistle herbivores can potentially affect the spread of a non-native thistle. Ecological Society of America Annual Meeting, Tucson, AZ.

## PROFESSIONAL EXPERIENCE

### TEACHING EXPERIENCE

- Insect Management Section of "Introduction to Organic Vegetable Production." Northampton County Cooperative Extension. 8/14/10, 8/13/11, and 8/11/12. Nazereth, PA.
- Biology for Elementary School Teachers Lab. (BIOS Q201; 12 Semesters) Associate Instructor. Indiana University. (2004-2010).
- Introductory Biology Lab (BIOS 101; 2 Semesters); Ecology and Evolution Lab (BIOS 302; 2 Semesters); Ecology Lab (BIOS 322; 2 Semesters) Teaching Assistant. University of Nebraska- Lincoln. (2000-2003).
- Plant Systematics Lab (BIOS 330; 1 Semester) Teaching Assistant. Bucknell University. (2000).

### TECHNICIAN EXPERIENCE

- 2011- 2013: USDA (Beltsville, MD), ARS, Sustainable Agricultural Systems Lab. (GS-9)  
Coordinated an agricultural experiment examining the role of cover crops on weed suppression and insect pest abundance on grain cash crops.
- 2003-2004: University of Vermont. Department of Botany and Agricultural Biochemistry.  
Monitored and maintained long-term demography plots of Slash Pine (*Pinus elliottii*) in Everglades National Park. Supervisor: Dr. Brian Beckage.

## AWARDS, GRANTS, FELLOWSHIPS, AND INTERNSHIPS

### EXTERNAL

- |            |  |
|------------|--|
| 2005- 2008 | Graduate Research Fellowship. The Land Institute.<br>\$14,000. |
| 2006       | Graduate Student Policy Award. Ecological Society of America.  |

2005	Travel Funds. Strategic Environmental Research and Development Program. \$1,000.
2001, 2002	Grants-in-aid of Research. Sigma Xi. \$300, \$300.
INTERNAL:	
2005, 2006, 2007, 2008, 2009	Floyd Plant Sciences Fellowship. Indiana University. \$2,700 or \$3,600/yr.
2008, 2009	Cleland Travel Funds. Indiana University \$500/yr.
2002	Research funds from George Lamb Memorial Scholarship Fund. University of Nebraska- Lincoln. \$1,011.
	Research funds from Initiative for Ecological and Evolutionary Analysis. University of Nebraska- Lincoln. \$114.
2001	Research Grant-In-Aid for Graduate Students. Center for Great Plains Studies. University of Nebraska- Lincoln. \$471.
	With K. Bradley: Research funds from George Lamb Memorial Scholarship Fund. University of Nebraska- Lincoln. \$1,500.
1998	Katherine Mabis McKenna Environmental Internship. Bucknell University. \$2,500.